Contextualizing waterscape health in a subtropical rangeland

By

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Thesis presented in partial fulfilment of the requirements for the degree of

Master of Science

at

Stellenbosch University

Conservation Ecology, Faculty of AgriSciences

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December 2021

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third-party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: December 2021

Abstract

Freshwater ecosystems are threatened globally by environmentally impactful agriculture. An ever-increasing population drives intensive agricultural production, putting immense pressure on freshwater ecosystem integrity. It is recognized that agriculture needs to be more environmentally sustainable. One way to achieve this is for agricultural production to align with, and support, local ecosystem functions while remaining within the other conventions (economic and social) of sustainable development. Livestock grazing areas (rangelands) are a major component of the total agricultural land use surface in Southern Africa. Within these rangelands, perennially inundated waterbodies across the landscape (waterscape) occur in a variety of hydrogeomorphic formats, both natural and artificial (depressions, deposition pools, weirs and dams) and are here referred to individually as waterbodies. Thus, the broad aim of this study is to gain some insight into the biotic and abiotic characteristics of waterscape health in rangelands of the Eastern Coastal Belt Ecoregion (ECBE).

Artificial waterbodies, like excavated depressions, constructed dams and weirs are common features in rural South African rangelands. Often, these excavated or constructed waterbodies completely modify characteristics of those that occur naturally, impacting waterscape ecosystem functions. However, artificial waterbodies can also be complementary to naturally occurring waterbodies in degraded waterscapes, improving overall waterscape biodiversity and resilience. In chapter 2, I compare environmental variables and dragonfly assemblage composition of natural and artificial waterbodies to demonstrate that intact, high order, naturally occurring forested stream deposition pools are an irreplaceable habitat for threatened aquatic biodiversity in the ECBE, vulnerable to impoundment and channel modification. I also show that well-managed excavated depressions provide valuable habitats for lentic biota in the region. I suggest agro-conservation strategies that aim to reduce disturbance frequency and channel modification in and around high order stream channels. Farm managers should promote artificial depressions outside of stream channels as a primary source of livestock drinking water.

Determining significant environmental and biological characteristics of healthy and compromised agro-ecological systems is vital to regional conservation planning and restoration. In chapter 3, I use the Dragonfly Biotic Index (DBI) to determine which biotic and abiotic variables drive waterbody health in the ECBE. I also illustrate the composition assemblage of dragonflies responsible for high and low DBI/ site scores. Again, I highlight the importance of reducing intensity and frequency of

livestock disturbance in stream deposition pools. I recommend considering individual waterbody habitat heterogeneity as a key feature in maintaining waterbody integrity. Invasive tree clearing and facilitating a compositionally and structurally diverse woody riparian component, appropriate for its hydrogeomorphic type is fundamental to regenerating ecosystem functions.

A transition towards sustainable livestock production means departing from resource intensive livestock systems. To achieve this, we need to identify appropriate scenarios for agroecology and contextualize agro-ecosystem. In the coastal plains of the ECBE, large savanna and azonal grasslands are suitable for well-managed ruminant livestock grazing, where ruminants play a vital role in maintaining ecosystem services. Here, analyzing local hydrogeomorphic features and biological attractors provides tangible methods to improve biodiversity conservation and perennial surface water resilience within a waterscape. This study also highlights that individual waterbody habitat heterogeneity is inimitable for biodiversity conservation at a global scale. I urge rangeland managers to consider and mimic all features of naturally occurring individual waterbodies within a waterscape for successful integration of rangelands and freshwater conservation. In the ECBE, extensive ruminant livestock keepers should increase frequency of depressions as a primary source of drinking water to reduce disturbance at streams.

This thesis is dedicated to those who inspire curiosity in agriculture, ecology, and the conservation of our precious earth.

Biogeographical sketch

Steve is a resident Wild Coast agroecologist with a passion rooted in exploring freshwater ecosystems in the region. Steve has studied a BSc in Natural Sciences at University of South Africa (UNISA) and a BSc in Agricultural Sciences at Stellenbosch University. His introduction to research in freshwater ecology was facilitated through the supervision of Dr Jeremy Shelton (Freshwater Research Centre); Olaf Weyl (RIP) from South African Institute for Aquatic Biodiversity (SAIAB),who raised the funding and sought the collaboration with the Stellenbosch University Department of Conservation Ecology to make the opportunity available to various South African Universities; and the Water Research Commission (WRC), where they assessed the first predation impact of non-native rainbow trout on a population of endemic Cederberg ghost frog in the Cape Floristic Region, South Africa. Steve is particularly interested in the ecology of freshwater ecosystems in agricultural landscapes and is currently completing his MSc at Stellenbosch University, where he is studying the relationship between dragonfly composition assemblages and agricultural land use in grazing areas around the Eastern Coastal Belt Ecoregion. Steve aspires to continue doing research in this biologically diverse area and is involved in several projects in his community aimed at facilitating landowner engagement, education, and awareness for freshwater conservation.

Acknowledgements

I wish to express my sincere gratitude and appreciation to the following persons and institutions in no specific order.

My partner in life, research and adventure, Caitlin Fisher, thanks for all your kindness, patience, enthusiasm, and overall assistance with this thesis.

My family, thanks for the incredible opportunity and support.

My supervisors Rhoda Malgas, Karen Esler, and Michael Samways, thanks for all the support, wisdom, and guidance.

Jeremy Shelton and the Freshwater Research Commission, thanks for the insight and guidance.

Terrence Bellingham, thanks for being such a legend and inspiration.

Charl Deacon, thanks for the valuable insight.

All my friends who helped in field and in life.

All the landowners, thanks for allowing and supporting this study.

Preface

This thesis is presented as a compilation of four chapters. Each chapter is introduced separately and is written according to the style of the African Journal of Aquatic Science (AJAS), to which the main data chapters, chapter 2, and chapter 3, will be submitted for publication. Because of this, some overlap is inevitable. The above-mentioned chapters offer insight into drivers and biological characteristics of South African waterscape conservation. The results from these chapters also contribute to an impressive global body of work studying Odonata as a group to better understand freshwater ecology.

Chapter 4 focuses on suitable practices for freshwater conservation in agroecology. The article uses the results from chapter 1 and chapter 2 of this thesis as a case study to advocate for contextualizing agro-ecological information. Also, the paper provides waterscape management and conservation strategies applicable across the globe.

A popular article adapted from chapter 4 will be submitted for publication in Farmers Weekly. This article offers tangible agro-ecological management recommendations for small ruminant livestock keepers in South Africa.

Chapter 1 - General introduction

No paper to be submitted for publication

Chapter 2 - Data chapter

Agro-ecological significance of natural and artificial waterbodies among rangeland waterscapes in the Eastern Coastal Belt Ecoregion, South Africa.

Chapter 3 - Data chapter

Biotic and abiotic characteristics of waterscape condition among rangelands in the Eastern Coastal Belt Ecoregion.Chapter 4 - General discussion

System specific management for rangeland waterscape conservation: A case study from the Eastern Coastal Belt Ecoregion.

Management and conservation strategies for resilient rangeland waterscapes.

Table of contents

List of figures

List of tables

Chapter 1

General introduction

The perilous state of freshwater ecosystems

Healthy freshwater ecosystems are both biologically and economically vital for human wellbeing. They provide clean water, food, livelihoods, and other ecosystem services worth US$4.0 trillion annually (Béné et al. 2016; Jackson et al. 2016). Yet freshwater ecosystems occupy less than one percent of the earth's surface and support over 10% of all known species (Dudgeon et al. 2006; Mittermeier et al. 2010; Strayer and Dudgeon 2010). Despite their overwhelming contribution to global biodiversity, freshwater ecosystems remain the most imperilled ecosystems in the world (Hitchman et al. 2018). The United Nations (UN) and World Health Organisation (WHO) have set a mandate (Sustainable and Millennium Development Goals) to urgently address the so-called "freshwater biodiversity crisis", highlighting the requirements of citizen-directed attention and appropriate research efforts (WHO 2008; Griggs et al. 2013; UN 2016; Darwall et al. 2018; Jucker et al. 2018; Albert et al. 2021).

Freshwater ecosystems are defined here as areas of marsh, fen, peatland, or open water, whether natural or artificial, permanent, or temporary, with water that is static or flowing, fresh, with no influence from tidal activity (Ollis et al. 2015). Three quarters of the world's freshwater ecosystems have been lost in the twentieth century (Davidson 2014). Consequently, it is estimated that populations of freshwater-dependent species have declined by 76% between 1970 and 2010, with a recorded 80% decline of vertebrates over the past 50 years, double the rate of either marine or terrestrial ecosystems (Dudgeon et al. 2006; Vaughan and Ormerod 2010; WWF 2016). Approximately one in three of the 28 000 freshwater-dependent species assessed are threatened with extinction (Darwall et al. 2018). The World Economic Forum (WEF) Global Risk Report (2021) places this biodiversity loss fourth in global impact risks, only after weapons of mass destruction, climate action failure, and infectious disease.

Freshwater ecosystems in agricultural landscapes

The perilous state of freshwater ecosystems can be largely accredited to a suite of basin, inter-basin, and global anthropogenic disturbances, that include aquatic habitat fragmentation and loss, hydraulic alteration, water pollution, and non-native species introduction (Dudgeon et al. 2006; Strayer and Dudgeon 2010; Garrow and Marr 2012; Matono et al. 2014; Weyl et al. 2020). Agriculture currently accounts for 70% of the world's freshwater use, and production is anticipated to double by 2050 in developing countries (Alexandratos and Bruinsma 2012). Agricultural land use is identified as a significant driver of environmental impact on freshwater ecosystems, via a multitude of complex pathways at numerous spatial scales (Foufoula-Georgiou et al. 2015; Dala-Corte et al. 2016; Chen et al. 2018; Melland et al. 2018). Agriculture can be defined in many ways and includes a variety of activities that affect freshwater systems, including those in South Africa.

Scientists and conservationists have encouraged modern agriculture to consider and incorporate the local ecological landscape (agro-ecosystems) into their agricultural practise at a case-specific level (Hering et al. 2015; Hathaway 2016; O'Brien and Arathi 2021). This type of contextualization allows the conservation of ecosystem services to be achieved through a regional landscape approach, moving away from blanket methods and towards "ecosystem innovation thinking" (Pigford et al. 2018, Marandure et al. 2018). There are several agricultural movements aimed at promoting agro-ecological systems that have sustained delivery of ecosystem services. For example, regenerative and restorative agriculture focuses on soil health and the restoration of agro-ecological systems (Sahu and Das 2020; Lal 2020). In savanna ecosystems, regenerative agriculture has shown that with appropriate management, grazing animals can sustain the delivery of clean drinking water from inundated waterbodies based on biodiversity maintenance of range-limited and sensitive aquatic biota, and maintenance of ecosystem resilience within the agroecological landscape (Teague and Kreuter 2020).

Small perennially inundated waterbodies, here referred to as waterbodies, are defined as areas smaller than two hectares, both natural (formed naturally without human intervention) and artificial (formed through human intervention), inundated with water all the time. (Samways et al. 2020). Waterbodies occur in a variety of hydrogeomorphic forms that are governed by differences in hydrology and geomorphology. For example, naturally occurring deposition pools in streams and rivers receive concentrated, diffuse water inflow and outflow through drainage channels, while depressions that occur naturally outside of channels are characterised by an entire elevated contour and receive surface and ground water infiltration from the substrate (Ollis et al. 2013). Waterbodies are artificial when they are constructed, either by modifying a stream channel to impound water or excavating a depression into the ground. All forms of waterbodies are common features in rangelands, collectively forming a rangeland waterscape. They provide drinking water for livestock, and appropriate habitat for aquatic biodiversity.

Artificial waterbodies can have major impacts on ecological functioning in a waterscape (Habets et al. 2018). In the same light, among degraded agricultural landscapes, they can provide refuges for aquatic biota (Samways et al. 2020). Complex synergies and trade-offs, as well as intricate driver pathways (e.g., indirect influences on the ecosystem), illustrate the need for more in-depth approaches and monitoring procedures that aim to disentangle the negative, positive, or neutral impacts of various co-occurring environmental stressors on waterscapes (Leitão et al. 2018). It is suggested that these procedures should include standardised and regionally suitable biological monitoring tools that can define the determining states of aquatic ecosystem functioning (O'Brien et al. 2016; Jackson et al. 2016).

Approaches to investigating land use impacts of freshwater ecosystem integrity

Hydrogeomorphology and hydrological regime determine waterbody structure, spatial arrangement, and connectivity (Arthington et al. 2006; Ollis et al. 2013). However, structural change that alters these driving forces can lead to changes in hydroperiod and depth of inundation, nutrient loads, physiochemical conditions, and both aquatic and riparian vegetation type and structure, amongst others (Ribeiro et al. 2016; Leitão et al. 2018). Landscape features and associated riparian vegetation also play a significant role in determining the structure of habitats in intermittent streams (Leitão et al. 2018), by moderating water temperature, filtering sediments, modulating water nutrient content, stabilising banks and surrounding land surfaces, and providing food and habitat to both aquatic and terrestrial organisms (Dudgeon et al. 2006).

Studying and comparing relative regional biological assemblage shifts in a system can be used as an effective indicator of habitat modification (Jackson et al. 2016). This is because they respond well to drivers of an ecosystem state which are often context dependent, complicated by synergistic, antagonistic and reversal effects from multiple stressors (Piggott et al. 2015; Jackson et al. 2016). Aquatic predators are important components of freshwater ecosystems as they are directly or indirectly connected to several ecosystem functions such as food webs, nutrient cycling, carbon cycling, habitat modification, and disease transmission (Hammerschlag et al. 2019). Predators also play a major role in maintaining ecological integrity of food webs and structuring prey communities and population dynamics. However, they are often the first to disappear with perturbation (Modiba et al. 2017). It is expected that waterbodies distressed by too frequent and intense disturbance from ruminant livestock will reduce the diversity of available habitat for aquatic biota, this will directly and indirectly alter the assemblage composition of resident aquatic apex predators.

Odonata (dragonflies and damselflies) are aquatic predators used to assess the state and integrity of waterbodies (Vorster et al. 2020). This is because at some stage in their life cycle they depend on an aquatic environment for their development and have been studied for their relative sensitivity to disturbance (Samways and Simaika 2016). They are also useful in indicating drivers of change, as they are taxonomically and phylogenetically highly diversified, exhibiting a wide variety of characteristics (e.g., size, diet, mobility, and behaviour) that directly relate to environmental parameters and central to provision of ecosystem services through mechanisms like the control of trophic networks and regulation of nutrient cycles (Rodrigues et al. 2019; Deacon et al. 2020; Bastos et al. 2021). In South Africa, the Dragonfly Biotic Index (DBI) uses a dragonfly's sensitivity to disturbance, geographic range, and International Union for the Conservation of Nature (IUCN) Red List status to assign each species a DBI score. The total assemblage composition DBI score is then divided by the species richness to determine a DBI/site score, comparable across sites in the same region (Simaika and Samways 2009).

Regionally specific, low-input, and restorative food production systems are expected to take a proactive part in feeding an increasing population (Teague 2018). To ensure that these agricultural transitions contribute to the sustainable provision of agro-ecosystem services, it is important to conduct research that guides the development of these agricultural entities and conservation synonymously (Graeub et al. 2016). Without such studies, there will remain a paucity of context specific, transferable information. The overarching aim of this study, therefore, is to gain some context with regards to characteristics of waterscape health in rangelands of the Eastern Coastal Belt Ecoregion (ECBE) using the DBI.

Thesis overview

In chapter 2, I ascertain the agricultural and ecological significance of natural and artificial waterbodies within rangeland waterscapes of the ECBE. I assess all natural and artificial waterbodies that are perennially inundated with water, for differences in environmental conditions and assemblage composition of dragonflies, while considering their hydrogeomorphic location. The results from this study indicate where natural waterbodies draw in high scoring taxa from a regional pool (i.e., are irreplaceable), and where artificial waterbodies contribute to waterscape conservation by providing a refuge for lentic taxa. This is explored by using a comparative study with biological indicators to test the null hypothesis that both artificial and natural waterbodies provide equally irreplaceable aquatic habitats among agricultural grazing areas in the ECBE.

In chapter 3, I determine which waterbody environmental variables, within their hydrogeomorphic zones (regardless of artificiality), encourage an assemblage composition of high-DBI dragonfly species. I use a comparative field assessment, between waterbodies, to analyse the relationship between DBI/site score and environmental variables within site hydrogeomorphic unit. I also assess the relationship between DBI/site and dragonfly presence and absence to identify which species were responsible for high and low DBI/site sores within each hydrogeomorphic location. The results from this study assist in identifying characteristic of waterbodies that promote high waterbody integrity, especially through presence of regional dragonfly attractors. This is achieved by testing the null hypothesis that within a given hydrogeomorphic unit, dragonfly assemblage composition will remain unchanged despite the condition of habitat.

In chapter 4, I discuss how contextualizing agro-ecosystem health is valuable in making suggestions as to the best practise management and restoration needs of rangeland waterscapes in the EBE. I argue that in the ECBE, considering regional waterbody hydrogeomorphic features and attractors of dragonfly species can direct management and restoration actions to improve the delivery of rangeland agro-ecosystem services and include farmers in the process. I discuss general features of global waterscape management and highlight more specific management procedures for conservation recommendation in the ECBE.

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Chapter 2

Agro-ecological significance of natural and artificial waterbodies among rangeland waterscapes in the Eastern Coastal Belt Ecoregion, South Africa

Abstract

Small perennially inundated waterbodies (waterbodies), both natural and artificial, are significant components of livestock-grazed agro-ecological systems in the Eastern Coastal Belt Ecoregion (ECBE), South Africa. They provide clean drinking water for livestock and contribute to the conservation of biodiversity and ecosystem resilience. Artificial waterbodies in degraded agricultural waterscapes can provide complementary habitat to natural waterbodies. Determining the significance of natural and artificial waterbodies as biological sanctuaries within rangeland waterscapes is of great conservation value in the ECBE. Dragonflies are used here to determine the extent to which natural waterbodies attract geographic range limited and sensitive taxa from the regional species pool (i.e., are irreplaceable). Additionally, I investigate the contribution made by artificial waterbodies in complementing the conservation value of the natural waterbodies. All natural and artificial waterbodies that are perennially inundated were assessed for differences in environmental conditions and assemblage composition of dragonflies. Results suggest that both natural and artificial waterbodies can provide irreplaceable biological refuges for aquatic biota. However, in both natural and artificial waterbodies, it is essential to provide certain hydrogeomorphic conditions that are vital for maintaining waterscape integrity and resilience. In the ECBE, natural deposition pools within tributary channels should be considered irreplaceable, while water storage features, like dams, constructed in tributary channels are harmful to the ecological integrity of the waterscape. Artificial depressions excavated outside channels are highly complementary to natural waterbodies within these rangeland waterscapes. Within river channels, conservation practitioners should design weirs that resemble natural deposition pools to improve local biodiversity.

Keywords: waterscapes, agroecology, waterbody design, weirs, Odonata

Introduction

Perennially inundated waterbodies, here referred to as waterbodies are small natural or artificial water bodies (< 2 ha) continually inundated with water (Ollis et al. 2013; Samways et al. 2020). A functionally connected group of waterbodies in the same location constitute a 'waterscape', contributing to the conservation of biodiversity and ecosystem resilience (Simaika et al. 2016; Deacon et al. 2018). Waterscapes support more aquatic biodiversity than solitary waterbodies (Oertli et al. 2002; Martinez-Sanz et al. 2012) and increase the area of occupancy for sensitive and range limited biota (Hill et al. 2016; Simaika et al. 2016; Deacon et al. 2018). Waterscapes as biological refuges are regionally specific and can be attributed to a variety of habitats, promoting heterogeneity at a landscape scale (Deacon et al. 2018; Kietzka et al. 2018; Jooste et al. 2020). Artificial waterbodies can provide complementary alternative habitats to naturally occurring waterbodies, especially within degraded agricultural areas (Simaika et al. 2016; Deacon et al. 2018; Briggs et al. 2019a; Samways et al. 2020).

Naturally occurring deposition pools in streams and rivers receive concentrated, diffuse water inflow and outflow through drainage channels (Ollis et al. 2013). These relatively small waterbodies are generally well vegetated and compositionally diverse, often occupied by endemic aquatic biota (Bonada et al. 2020; Cantonati et al. 2020). Substrate composition of such pools are largely governed by the hydrological regime and organic matter input (Hauer et al. 2018). High flow velocities generally transport larger grain sizes, such as boulders and cobbles (Hauer et al. 2018). Pools located in smaller channels, like small tributary streams, have lower flow velocities, and typically support fine sediments like pebbles, sand, and silt (Hauer et al. 2018). Pools that have very low or no flow accumulate organic matter and turn into a muddy benthic environment (Hauer et al. 2018). In contrast, depressions that occur naturally outside of channels receive surface and ground water infiltration from the substrate (Ollis et al. 2013). These vernal waterbodies often dry out during prolonged periods of no or low rainfall and are vulnerable to disturbance from agricultural activity (Samways et al. 2020).

Within extensive agricultural grazing areas, waterscapes provide drinking water for livestock. Artificial waterbodies are often constructed in these grazing landscapes to provide additional water storage (reservoirs/ dams) or for managing water levels (weirs) and tend to replace small natural waterbodies like depressions and stream deposition pools (Samways 1989; Apinda-Legnouo et al. 2013; Bichsel et al. 2016). Artificial waterbodies are usually constructed by obstructing channel flow or by excavating a depression outside of a river channel. These artificial waterbodies are often regularly disturbed, and have low quality aquatic and riparian habitats, as evidenced by their homogeneity and overall low diversity of riparian and macrophyte vegetation (Deacon et al. 2018). In contrast, waterbodies with high and constant water levels maintain high levels of vegetation diversity and are often attractive to many aquatic species (Janssen et al. 2018; Briggs et al. 2019b; Jooste et al. 2020).

Taxonomic groups that are comparable at spatial and temporal scales and easily identified in field by non-specialists are becoming increasingly popular for monitoring freshwater ecosystem condition (Jackson et al. 2016). Dragonflies (Odonata), including both damselflies (Zygoptera) and dragonflies (Anisoptera), are here collectively referred to as ‘dragonflies’. They are excellent indicators of habitat quality, being variably sensitive to local environmental changes, are well-studied taxonomically, highly visible, widely distributed, and have life cycles with both aquatic (larval) and terrestrial (adult) stages (Simaika and Samways 2009; Kietzka et al. 2021). Adults are highly mobile and respond strongly to changes in habitat condition, whether improving or declining, leading to shifts in assemblage composition when environmental conditions change (Samways and Sharratt 2010; Simaika et al. 2016; Kietzka et al. 2017; Kietzka et al. 2018; Deacon et al. 2020). The Dragonfly Biotic Index (DBI) is a tool used in South Africa whih incorporates the sensitivity, distribution, and threat status of adult male dragonflies to assess the relative ecological state of a waterbody. Details on the DBI are provided in the methods of this study.

Studies on dragonfly response to land transformation in South Africa have shown: 1) adult Odonata respond to changes in water quality and vegetation composition (Kietzka et al. 2017; Modiba et al. 2017), 2) land transformation significantly influences dragonfly assemblages but does not always significantly reduce species diversity (Kietzka et al. 2018; Deacon et al. 2019; Jooste et al. 2020), and 3) artificial waterbodies can have similar environmental components to those that occur naturally and that habitat heterogeneity within a waterscape increases the area of occupancy of species by up to 75% (Deacon et al. 2018; Jooste et al. 2020).

A regionally specific understanding of how natural and artificial waterbodies act as biological sanctuaries within grazing waterscapes is of great conservation value. It can allow us to conserve biological diversity while providing drinking water to grazing animals. Chintsa Bay lies within the Amatole-Kei catchment district and falls under the Great Kei local Municipality (GKM**).** The GMK covers an area of 1 421 km^2 with approximately 96% of this land used for agricultural production, 77% for livestock (mostly cattle, some sheep, goats and game) and 33% a mixture of crop production, hydroponics and dairy (Great Kei Municipality 2017). Although agriculture is generally small scale, it is both subsistence and commercial (Great Kei Municipality 2017). Considering the area's proximity to the city of East London, livestock farming is a prominent form of economic gain in the region. If we can illustrate where naturally occurring waterbodies are irreplicable and demonstrate situations where artificial waterbodies are beneficial for sustaining biodiversity, farmers and conservationists can work toward preserving and restoring diverse and resilient agro-ecological waterscapes in the Eastern Coastal Belt Ecoregion (ECBE).

While there is agreement as to the potential conservation value offered by artificial waterbodies at a global scale (Hill et al. 2018), this has not yet been explored in the ECBE. There is a need in this region for research that identifies effective conservation measures that can be harmonized with agricultural management. The broad aim here is to gain insight into the relative significance of natural and artificial waterbodies in rangeland waterscapes of the EBE. This is explored by using a comparative study with biological indicators to test the null hypothesis that both artificial and natural waterbodies provide equally irreplaceable aquatic habitats among agricultural grazing areas in the ECBE. Specifically, three questions are posed:

a) Is there significant variation in the sets of habitat characteristics between artificial and natural waterbodies among agricultural grazing areas in Chintsa Bay, ECBE, South Africa?

b) Is there significant variation in dragonfly assemblage composition and species diversity between naturally occurring and artificial waterbodies in agricultural grazing areas in the area?

c) Is there significant variation in Dragonfly Biotic Index site scores (see below) between naturally occurring and artificial waterbodies among agricultural grazing areas in the area?

Materials and methods

Study area

Chintsa Bay (32°50' S; 28°60' E; Figure 2.1b) has a total catchment area of 288 km^2 and encompasses the outlets of the Cunge River, Chintsa River, Chefani River; Kwenura River and Nyara River. The top of the catchment is at approximately 400 m.a.s.l., and the rivers flow intermittently in a S-SE direction, through deeply incised valleys between 1 km and 12 km in length. The focal area here is the coastal plain of Chintsa Bay, including waterbodies associated with the Chintsa River, Cunge River and Chefani River catchments (Figure 2.1c). The area has a mild subtropical climate with few extremes and very little to no frost, due to its closeness to the Indian Ocean (Mucina and Rutherford 2006). The temperature ranges from 5.3°C to 32°C (Mucina and Rutherford 2006). Chintsa Bay receives most of its rain during spring and early to mid-summer, though rain occurs in lesser quantities throughout the year. The average annual rainfall is between 900-960 mm (Kleynhans et al. 2005; Mucina and Rutherford 2006).

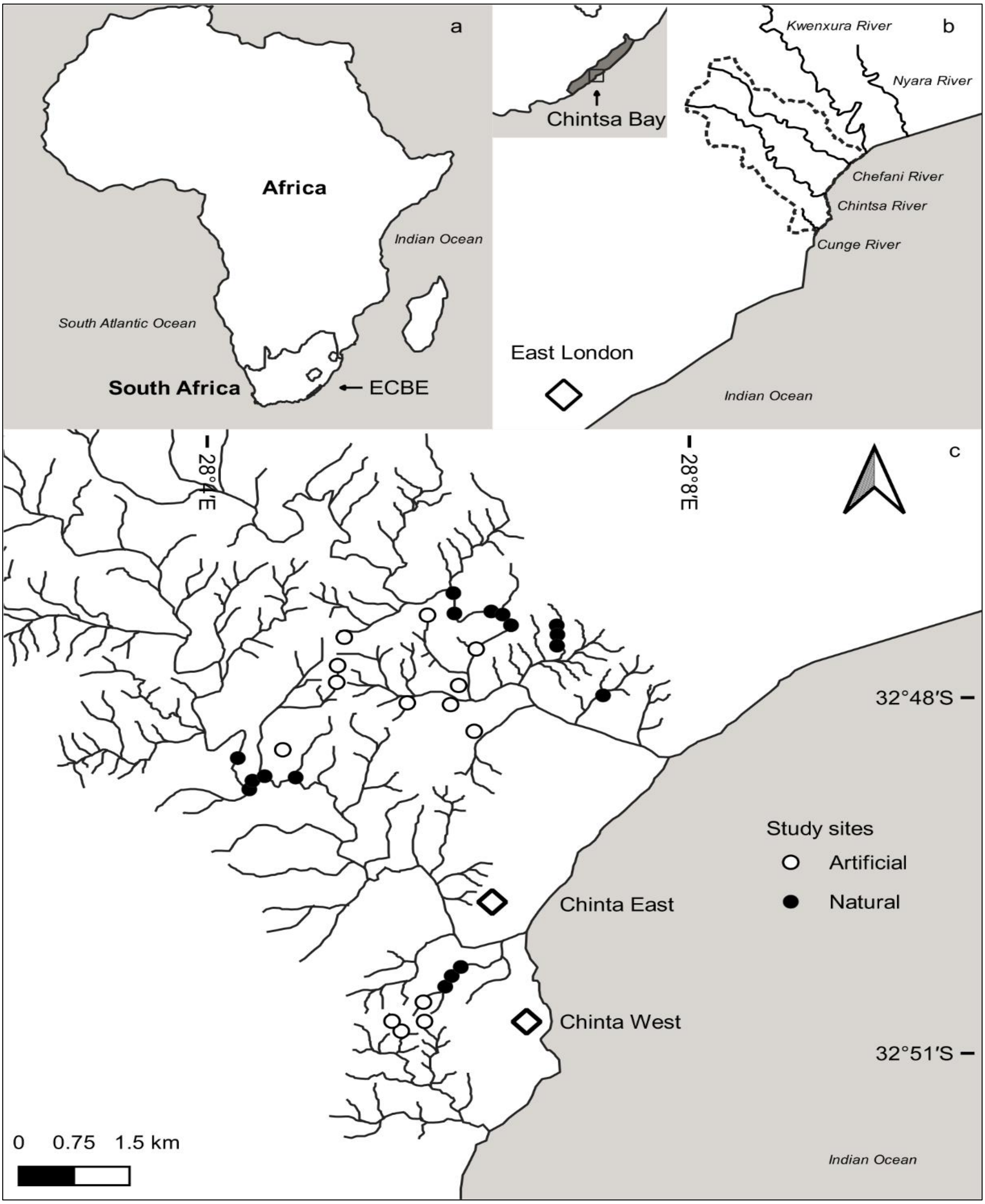

Figure 2.1: Location of a) the Eastern Coastal Belt Ecoregion (ECBE), South Africa, b) Chintsa Bay and major rivers, with focal catchment of study delineated by dashed border, and c) Sampling sites within the region. Dark circles represent naturally occurring waterbodies, and light circles represent artificial waterbodies. Names of towns are shown

Chintsa Bay lies within the Maputuland-Pondooland-Albany Global Biodiversity Hotspot (Myers et al. 2000) and forms a transition zone between Albany Thicket (AT), Indian Ocean Coastal Belt (IOCB) and Savannah (S) Biomes (Mucina and Rutherford 2006). Vegetation in and along broad, extensive river valleys is described as Buffels thicket of the AT biome (SANBI 2018). While in steeper gorges along riparian zones the vegetation is classified as scarp forest of the IOCB (SANBI 2018). Vegetation on valley tops, coastal plains and in loamy soil are classified as either bisho thornveld, eastern coastal thornveld, or eastern valley bushveld of the S Biome (SANBI 2018). Due to the transitional nature of this landscape, disturbances such as fire and grazing lead to shifts in biological community structure, resulting in a mosaic of these vegetation types (Mucina and Rutherford 2006).

Freshwater habitats in the ECBE host a rich assemblage of aquatic biota with several ancient and endemic species (Kleynhans et al. 2005). Additionally, the riparian forests are a hotspot for terrestrial biodiversity and support many endemic and threatened taxa (Mucina and Rutherford 2006). In many areas of the ECBE, dragonflies are poorly studied, with no detailed studies to date on dragonfly ecology in the Chintsa Bay area. Given the variety of ecosystems in the area, it is likely that the dragonfly assemblages are highly variable at a landscape scale (Nagy et al. 2019).

In addition to the field guides of Southern Africa (Samways 2008; Underhill et al. 2018; Tarboton and Tarboton 2019), citizen science records on iNaturalist (2020-2021) show a variety of sensitive and specialist species in the area, as well as some species outside of their recorded core geographic range. For example, *Chlorolestes tessellatus* (Burmeister, 1839) (Figure 2.2a), is a South African endemic forest specialist that requires shade and stream banks dominated by indigenous vegetation (Samways 1999). Also recorded in the area are savanna residents like *Brachythemis leucosticta* (Burmeister, 1839); *Orthetrum stemmale* (Burmeister, 1839), *Diplacodes luminans* (Karsch, 1893), and *Palpopleura lucia* (Drury, 1773), known to utilize open shallow marsh areas (Samways and Simaika 2016; Tarboton and Tarboton 2019). Lastly, a rare and sensitive species, *Metacnemis valida* (Hagen in Sélys, 1863) (Figure 2.2b), is a narrow range, Albany Thicket endemic, listed as Endangered on the IUCN Red List (IUCN 2021) (Figure 2.2b). This species inhabits slow or still reaches of rivers with substantial indigenous riparian vegetation. It is threatened by habitat degradation, especially encroachment by invasive alien trees.

Figure 2.2: a) Rare Eastern Cape heavily banded form of forest specialist damselfly *Chlorolestes tessellatus*; and b) The endangered and endemic damselfly, *Metacnemis valida*.

Site selection

One of the challenges to making inferences about ecological conservation from a comparative study that uses biological indicators, is accounting for confounding factors outside of the measured variables. I attempted to account for these factors in three ways. Firstly, all sites were chosen in an area that would be representative of a regional dragonfly pool (Samways and Simaika 2016) within areas with typical extensive agricultural grazing scenarios and little alternative forms of disturbance, such as cultivated land or urban development. Secondly, a range of environmental variables that are known to influence dragonfly assemblages were measured and the related indices assessed. Thirdly, only sites known to be free of alien predatory fish were included. This information was ascertained by interviews with landowners as well as by mounting underwater cameras in river deposition pools, for 20 min at three separate locations, as predatory fish can have confounding influences on stream communities (Shelton et al. 2015; Avidon et al. 2018; Weyl et al. 2020).

Sixty-four potential study sites (perennially inundated waterbodies) were delineated in three hydrogeomorphic locations (river deposition pools, tributary deposition pools and out of channel depressions) using GIS software (QGIS development team 2021) and prior knowledge of the area. A series of preliminary field investigations were employed during periods of low rainfall (May 2018-October 2019) where relevant zones were traversed, and appropriate inundated waterbodies were identified and confirmed with landowners where possible. A total of 32 waterbodies out of the 64 preliminary sites were found to be perennially inundated with water and were selected as suitable sites for this study. Eleven sites in river channels (Figure 2.3a), 14 in tributary channels (Figure 2.3b), and 7 outside of any channel (Figure 2.3), both natural (18) and artificial (14). Artificial waterbodies were constructed waterbodies characterized by the presence of an artificially created barrier obstructing water flow or excavation of a depression outside of a channel. All sites were located on privately owned land with extensive cattle grazing scenarios typical of the area. In some areas, sites were located where landowners have spent considerable effort in maintaining an idea of integrity of their grazing landscape, while others were in areas with long histories of frequent grazing disturbance.

Figure 2.3: Typical sampling sites (small perennial waterbodies) of different types (artificial and natural) in relative hydrogeomorphic locations. a) is a weir (artificial) located within a river channel, b) a typical well-forested stream deposition pool within a tributary channel, and c) an artificial depression outside of a channel

Dragonfly surveys

Adult dragonflies were sampled according to procedures of the Dragonfly Biotic Index (DBI), which uses principally adult male dragonflies as a measure of ecological integrity (although female adults, larvae and exuviae can also be used to supplement the adult male data) (Samways and Simaika 2016). Each species is assigned a score ranging from 0 to 9, based on its geographic range, threat status (according to the IUCN Red List), and sensitivity to habitat change. A score of 0 refers to geographically widespread, non-threatened, habitat generalist (including occupying artificial habitats) species. In contrast, a score of 9 refers to geographically highly restricted, IUCN red-listed, and habitat sensitive species. The total DBI score at each site is divided by species richness to give a DBI/site score. This score assesses and enables a comparison of the focal ecosystems. There is a highly significant correlation between DBI/site scores and other popular freshwater health index scores, like the South African Scoring System (SASS) (see Dickens and Graham 2002), used in South Africa (Simaika and Samways 2011; Rosset et al. 2013; Kietzka et al. 2019).

Before sampling took place, a pilot study was done to ensure accuracy of identification (Samways and Simaika 2016). The first standardized sampling session took place on calm ($< 3.5\ m{\cdot}s^{-1}$) and sunny days between 10:00 and 15:00 from January to March 2020, the optimal flying time for most dragonflies (Samways 2008; Modiba et al. 2017; Tarboton and Tarboton 2019). Dragonflies were caught with a net, photographed, and released without notable harm, with a permit provided by the Department of Economic Development, Environmental Affairs and Tourism (DEDEAT). Sampling was around the entire perimeter of the waterbody recording dragonfly individuals both on the bank and into the water, up to 10 m distance away from the wetted edge, over 60 minutes. Species accumulation curves as per Modiba et al. (2017) showed that this sampling procedure is adequate for determining diversity of species at a site. A second sampling session at every site was conducted between April and May 2020 to note any additional species present.

Environmental surveys

Water quality parameters were measured at each site following the dragonfly surveys. Four physio-chemical variables describing water quality, and known to affect dragonfly assemblages, were measured (Kietzka et al. 2017; Deacon et al. 2020). These variables were water temperature (°C), pH, electrical conductivity (EC; $\mu S/cm^{-1}$), and total dissolved solids (TDS; ppm) and were measured using a Hanna combo tester HI 98129 at three random points at each site.

In situ measurements of wetted edge width (m) were made across three equidistant transects of the waterbodies measured length (m). Water depth (cm), substrate type based on particle size (bedrock - indeterminable; boulder > 256 mm; cobble 64-256 mm; pebble 4-64 mm; gravel 2-4 mm; sand < 2 mm, but grains detectable; silt and mud, grains not detectable), and canopy cover (presence/absence) were determined at five equidistant points along the three width transects laid across each waterbody's longest dimension. This design resulted in 15 data points for each of these variables per site. Water depth was measured using a calibrated depth rod placed vertically on the waterbody bed at each point along the width transects. This provided six measurements for both the outer most depths and mid-outer depths, and three measurements for the middle depth at each site. Substrate type was determined at each point where the rod hit the waterbody bed by identifying the substrate (based on its size) at point of contact with aid of an appropriate key (see Ollis et al. 2013). The percentage of substrate cover was then estimated by quantifying the amount of each substrate type identified at the 15 data points. Likewise, percentage canopy cover at each site was derived from the amount of canopy cover observed directly above each of the 15 data points taken along the three width transects.

Percentage cover of aquatic vegetation (free floating; floating attached/rooted; submerged; algae mat) and herbaceous vegetation (Poaceae spp. Cyperaceae spp. Eriocaulaceae spp. herb/forb, geophyte, Juncaceae spp. and Typhaceae spp.), was estimated by dividing the waterbody surface water and saturated soil area into equal size quadrats and determining the proportion of vegetative cover (see Ollis et al. (2013) for percentage cover estimation key). The same key was used to estimate the percentage cover of riparian canopy height classes (0-1 m, 1-4 m, 4-7 m, 7-10 m, >10 m) and woody exotic riparian vegetation, within a 10 m distance of the waterbody dry soil area. Aquatic vegetation parentage cover was determined to quantify the characteristic macrophyte assemblage composition at each site.

To analyse waterbody environmental variables, each site was classified according to its type (natural or artificial) and hydrogeomorphic location (within a river channel, tributary channel, or outside of a channel). Average depth (cm), average outer depth (cm), average mid-outer depth (cm), and average middle depth (cm) of each waterbody was estimated by using their respective five equidistant transect depth measurements. Water surface area (m^2) was estimated by multiplying the waterbody wetted length by the average wetted widths. Volume (m^3) of waterbody water was estimated by multiplying the surface area by average depth.

Statistical analysis

Variation in environmental variables between natural and artificial waterbodies

A Principal Component Analysis Biplot (PCA biplot) (Gower and Hand 1996), based on the measured environmental variables, was used to visualize relationships between sites. A correspondence coefficient (r^2) of 0.4 and -0.4 between principal components was used to reduce variables to a limited number of independent, correlated parameters that summarise major axes of environmental variation among sites. An alpha ellipsis of 0.5 was used in the biplot to highlight concentrations of sites with similar variables.

To assess the variation in sets of environmental variables between waterbody types, a mixed model ANOVA was used in a pairwise manner, i.e., each environmental variable was analysed against site type separately. The mixed model ANOVA tests whether either of the main effects (site type and hydrogeomorphic subclass) or the interaction of the two is statistically significant in explaining variation between measured variables. The mixed model ANOVA was used to assess whether there was significant variation in environmental variables between waterbody types while considering the confounding influence of hydrogeomorphic sub-class.

Prior to the ANOVA, environmental variables were plotted against a theoretical normal distribution and observed for trends in normality (Das and Imon 2016). Environmental variables that deviated from a normal distribution were assessed using a non-parametric Mann–Whitney test (Wilcoxon 1946; Mann and Whitney 1947). A Levene's test (Levene 1960) was then conducted to assess the equality of variances among measured variables. For parameters with heterogenous variation, a Welch's t-test (Welch 1951) was used.

Characterizing and contrasting dragonfly composition between natural and artificial sites

Cross tabulation analysed with a Fisher–Exact test (Fisher 1934) was used to determine if presence or absence of dragonfly species at natural and artificial waterbodies was due to non-random associations. To visualize how strongly species presence and absence was related to waterbody type, a correspondence analysis was conducted, and a plot was constructed using one principal component.

Comparing species diversity between natural and artificial waterbodies

Species diversity at each site was determined by counting the diversity of dragonfly species present during sampling. First, species diversity was plotted against a theoretical normal distribution and observed for trends in normality (Das and Imon 2016). Significant variation in species diversity between site types was determined using a mixed model ANOVA. A Levene's (Levene 1960) test was then conducted to assess the equality of variances among measured variables. A Fisher LSD post hoc test was conducted to determine if the significant effect from the ANOVA was due to waterbody type. To visualize the differences in species diversity between waterbody types, a box and whisker plot was used. To visualize the relationship between individual sites, their type, and species richness a principal component biplot was constructed using shapes to indicate site type and colour scale to indicate species richness.

Comparing Dragonfly Biotic Index site scores

To determine the DBI/site score, the sum of the individual species' DBI scores at each site was divided by the species richness (Samways and Simaika 2016). These DBI/site scores were plotted against a theoretical normal distribution and observed for trends in normality (Das and Imon 2016). Variation in DBI/site scores were then assessed between waterbody types using a mixed model ANOVA. A Fisher LSD post hoc test (Williams and Abdi 2010) was conducted to determine if the significant effect from the ANOVA was due to waterbody type. A Levene's test was then conducted to assess the equality of variances (Levene 1960). A box and whisker plot were constructed to visualize the differences in DBI/site score between waterbody types. To visualize the relationship between individual sites, their type, and DBI/site scores a principal component biplot was constructed using shapes to indicate site type and colour scale to indicate species richness.

Software used

Ordination, ANOVA and assumption tests were conducted using R 4.0.2 statistical software packages: '*base R*' (R core team 2013), '*vegan*' (Dixon 2003) and '*ggplot*2' (Wickham 2011). Fisher–Exact test was conducted using: 'TIBCO Statistica' analytical software.

Metadata

Metadata describing the site information, environmental variables and dragonflies recorded can be found at: https://figshare.com/s/71f3582c403de9832203

Results

Multivariate analysis of waterbody types

Twenty of the measured environmental variables were significantly different between natural and artificial waterbodies, despite their hydrogeomorphic location (Table 2.1). Sixteen of these environmental parameters had moderate to strong ($-0.40 > r^2 > 0.40$) relationships between principal components, visually represented in Figure 2.4. Sites were distinctively separated in a multivariate habitat space, indicating consistent differences between site types. These separations were highlighted by 0.5 alpha ellipses. One site, an artificial river deposition pool (weir), overlapped with the ellipsis of natural sites and had environmental characteristics like waterbodies that occur naturally. Two naturally occurring river deposition pools were separated from the other natural sites and had different environmental characteristics.

Artificial sites were usually larger, deeper, and held more water. Also, they were generally warmer with lower concentrations of total dissolved solids (TDS) and had lower electrical conductivity (EC). The benthic environment of artificial sites was mostly muddy, while natural waterbodies were diverse with considerable amounts of rocky substrata (gravel, pebbles, and bedrock). This was mostly prevalent within tributary channels, and although larger, the weir had physio-chemical properties (temperature = 25.1 °C, TDS = 216 ppm and EC = 434 $\mu S/cm^{-1}$) and a large component of bedrock (40%) as substrate, similar in physical composition to other natural river deposition pool sites.

The amount and types of aquatic and herbaceous macrophytes differed significantly between waterbody types. Generally, natural sites had a low percentage cover but consistently diverse assemblage of marginal vegetation, with low percentage cover of aquatic vegetation. In contrast, artificial sites were dominated by vegetation cover of a less diverse array of both aquatic and marginal vegetation that included Cyperaceae spp. Poaceae spp. and Juncaceae spp. Two naturally occurring deposition pools contained considerable aquatic vegetative cover, like artificial sites. A single artificial river deposition pool site (weir) had a substantially diverse composition of marginal vegetation cover and no aquatic vegetation, like other river deposition pools.

One of the major differences in environmental variables among site types was the riparian environment. The riparian vegetation of artificial waterbodies was dominated by low stature (1-4 m) plants, with a high percentage cover of riparian exotic vegetation that offered little canopy cover. This contrasted with natural waterbodies where riparian vegetation was structurally diverse (riparian canopy cover height represented at all levels at each site), mostly consisting of trees (4-10 m) offering high canopy cover in places. The one exception to this was the weir, which had a structurally diverse riparian forest, like other naturally occurring river deposition pools.

Table 2.1: environmental variable means and standard errors of sites with statistically significant ($p < 0.05$) variation in environmental variables between waterbody types (natural or artificial) sampled around Chintsa Bay, South Africa (2020)

	Artificial		Natural	
	mean	SE	mean	SE
Temperature (C°)	30.61	0.68	26.65	3.90
Total dissolved solids (ppm)	188.50	38.37	289.92	68.33
Electrical conductivity (µm)	376.80	76.61	790.55	135.97
Surface Area (m^3)	6094.45	1179.61	1363.00	514.18
Average depth (cm)	61.14	7.60	34.45	6.41
Mid-outer depth (cm)	74.38	8.65	38.37	6.89
Volume (m^3)	408710.07	99034.38	84833.53	51920.74
Poaceae spp. (%)	20.07	3.41	6.39	1.45
Eriocaulaceae spp. (%)	0.57	0.40	3.06	0.59
Geophyte spp. (%)	0.57	0.40	4.31	1.21
Juncaceae spp. (%)	12.11	3.12	3.47	1.80
Riparian vegetation 0-1 m (%)	61.43	7.06	16.11	4.65
Riparian vegetation 4-7 m (%)	7.86	3.54	28.61	5.25
Riparian vegetation 7-10 m (%)	5.36	2.59	28.06	5.47
Canopy Cover (%)	7.14	2.84	49.63	7.76
Bedrock (%)	3.81	2.86	44.07	5.63
Mud (%)	75.71	7.58	10.37	2.96
Gravel (%)	0.95	0.95	21.11	4.01
Pebbles (%)	0.00	0.00	2.22	0.76
Cobbles (%)	0.48	0.48	8.15	0.76

SE = Standard error of the sample.

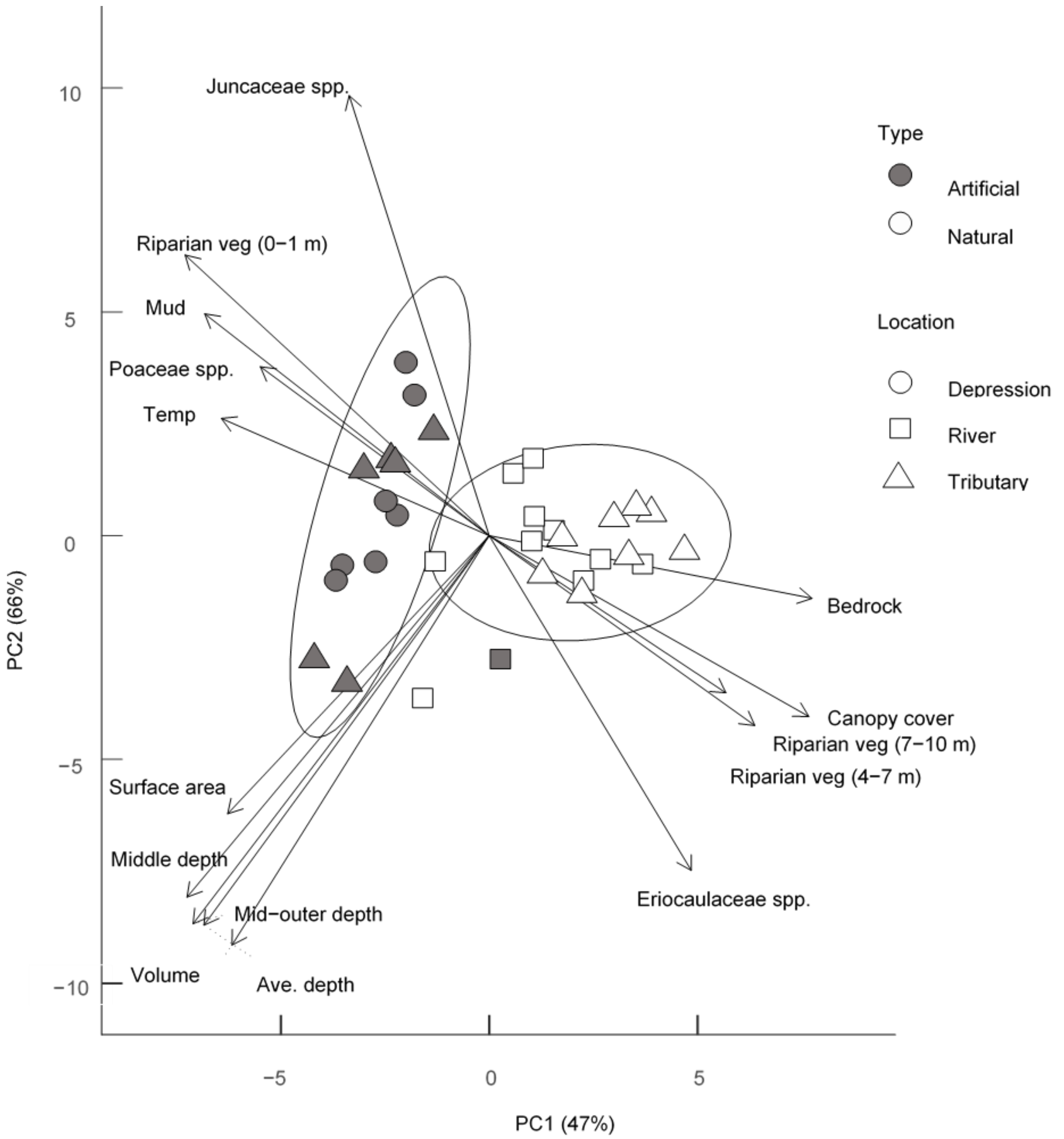

Figure 2.4: Principal Component (PC) biplot summarizing differences in environmental conditions between natural and artificial waterbodies within their relevant hydrogeomorphic location. The length and direction of vectors (solid black lines) indicate the relationship between environmental variables, as well as the direction and strength of influence of each environmental variable on the variation in overall environmental conditions among sampling sites

Composition of dragonfly assemblages between natural and artificial sites

A total of 37 dragonfly species were recorded at the 32 study sites (Figure 2.5). The presence and absence of 10 species were significantly ($p < 0.01$) separated by waterbody type (Table 2.2). One species, *Chlorolestes tessellatus*, only occurred in deposition pools. *Chlorolestes tessellatus* is a shade adapted species with a relatively narrow distribution in forested areas.

Nine species were specifically associated with artificial waterbodies (Table 2.2). Four of these species (*Ischnura senegalensis*, *Sympetrum fonscolombii*, *Crocothemis erythraea* and *Anax imperator*) are widespread generalists, occupying most open still water habitats. Five dragonfly species recorded in artificial waterbodies (*Lestes tridens, Ceriagrion glabrum, Diplacodes luminans, Tramea limbata and Brachythemis leucosticta*) are principally savanna residents. Four of the dragonflies, one generalist (*I. senegalensis*) and three savanna specialists (*B. leucosticta, T. limbata* and *D. luminans)* were only present outside of channels or at artificial waterbodies within channels.

Not statistically significant (only 1 or 2 observations) but noteworthy for this study, was *Metacnemis valida* (with a DBI top score of 9), was recorded in a weir (artificial) along a river channel, and *Orthetrum stemmale* in two artificial waterbodies outside a channel.

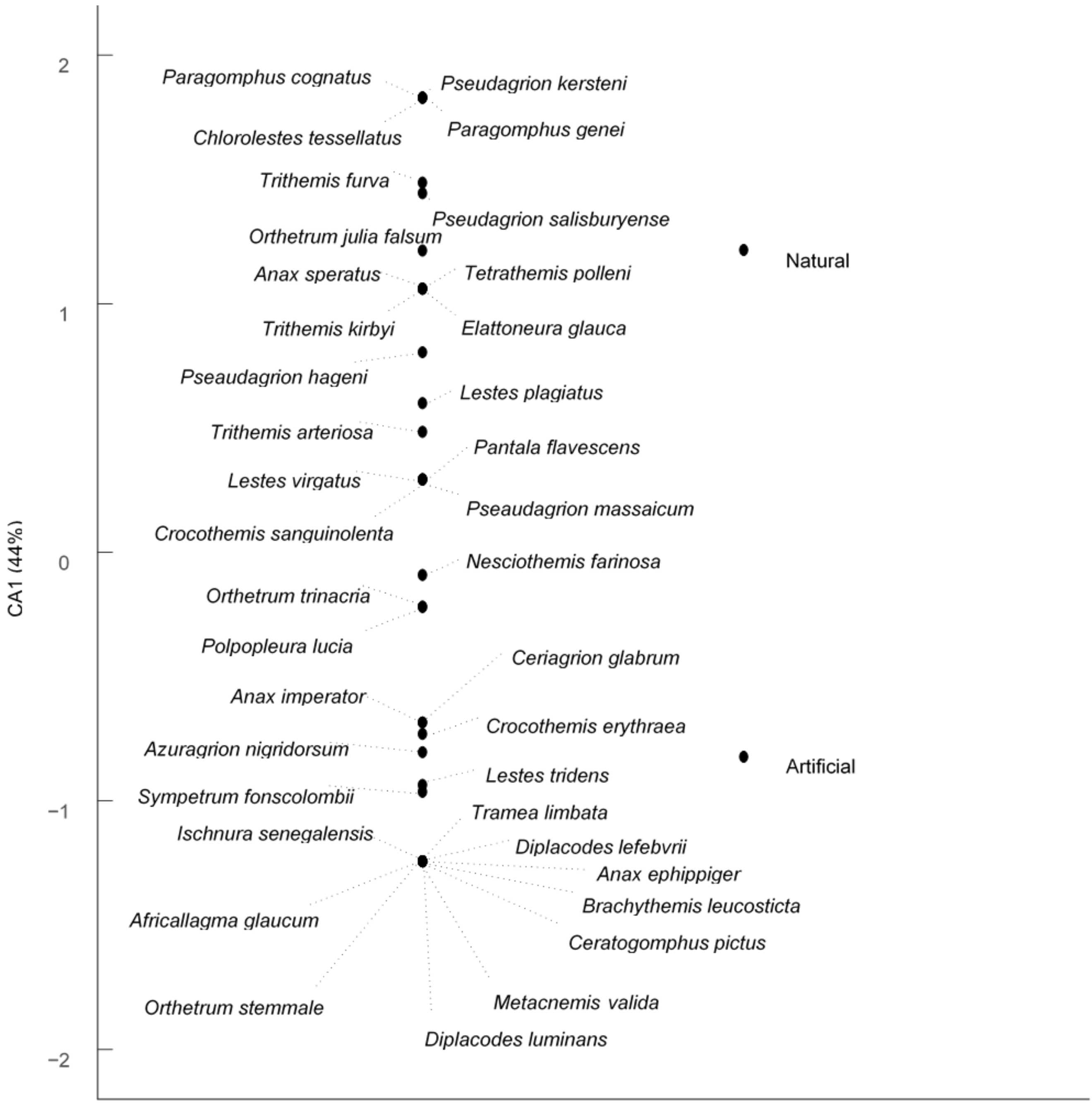

Figure 2.5: Correspondence Analysis plot illustrating the relationships between waterbody types and occurrence i.e., presence and absence of dragonfly species sampled at each site. Coordinates were extracted from dimension 1 of a correspondent analysis (CA) and plotted on the y axis. Random coordinates were used on the x axis for waterbody type and dragonfly species. Dotted lines were used to indicate a species position and avoid overlapping of labels.

Table 2.2: results of Fisher-Exact test showing significant (p < 0.01), non-random associations between waterbody type and occurrence of dragonfly species with associated Dragonfly Biotic Index indices and habitat information sampled around Chintsa Bay, South Africa (2020)

	Habitat preference	HGM	Eco-reg	Threat status	Dist	DBI	$\chi 2$
Natural							
Chlorolestes tessellatus	Forest	Trib; riv	14	0	2	4	17.13
Artificial							
Ischnura senegalensis	All open water	Trib; dep	29	0	0	0	30.86
Sympetrum fonscolombii	All open water	All	23	0	0	0	16.71
Lestes tridens	Savanna	All	10	0	2	3	13.78
Ceriagrion glabrum	Savanna	All	20	0	0	0	10.38
Diplacodes luminans	Savanna	Trib; dep	11	0	1	3	16.87
Tramea limbata	Savanna	Trib; dep	14	0	0	0	14.21
Crocothemis erythraea	All open water	All	28	0	0	0	13.03
Brachythemis leucosticta	Savanna	Trib; dep	16	0	1	2	11.06
Anax imperator	Temporary open water	All	22	0	0	1	10.38
*Metacnemis valida**	Pristine rivers	Riv	5	3	3	9	N/A
*Orthetrum stemmale**	Savanna	Dep	8	0	2	4	N/A

* Not statistically significant (p > 0.05; CI: 95%); HGM = hydrogeomorphic location (trib = tributary deposition pool, riv = river deposition pool; dep = out of channel depression); Eco-reg = ecoregions occupied, DBI = Dragonfly Biotic Index score; Dist = DBI distribution score

Species richness

Species richness was significantly different (F = 12.32 (1, 28); $p < 0.01$) between natural and artificial sites, despite hydrogeomorphic location (Figure 2.6). Generally, artificial waterbodies had a greater diversity of species at each site, mean (SD) = 10.43 (±3.55), than naturally occurring waterbodies, mean (SD) = 5.33 (±4.50). Compared to artificial sites (min = 4, max = 16, range = 10), naturally occurring sites had a wider range of species diversity (min = 1, max = 17, range = 16). The weir site had a similar species richness (14) to other natural sites in river channels with high species richness, mean (SD) = 8.5 (±3.50), which was also like artificial sites in tributaries and depressions, mean (SD) = 10 (±3.29). These sites all had considerably higher species richness than natural sites in tributaries, mean (SD) = 1.37 (±1.06).

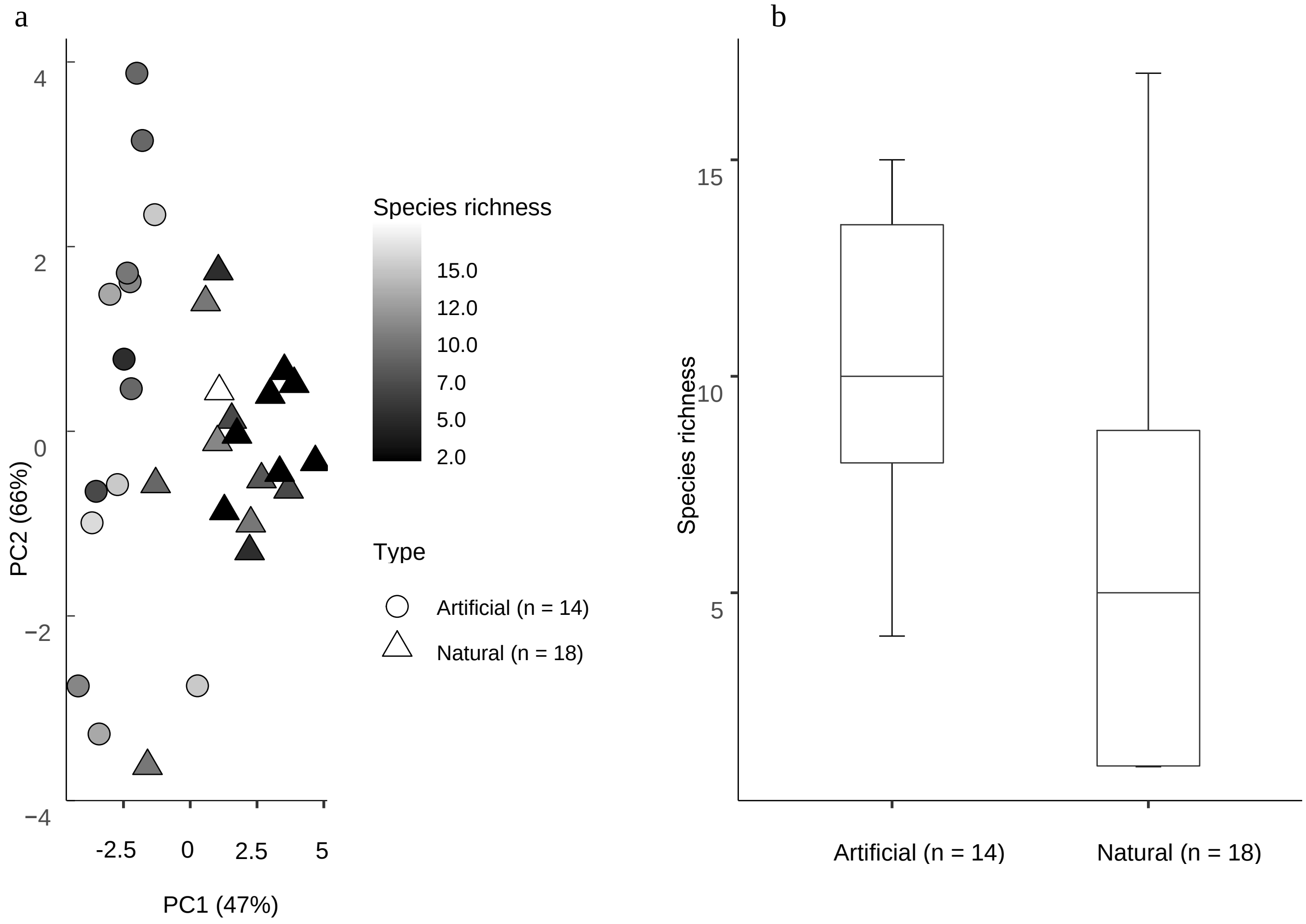

Figure 2.6: a) Principal component (PC) biplot illustrating the relationship between differences in sites according to environmental variables (distance between points), site types (shape) and species richness (colour scale). b) Box and whisker plot showing differences (minimum, maximum, mean, first and third quartile) in the dragonfly species richness between artificial and natural waterbodies.

DBI/site scores

The DBI/site scores were significantly different ($F = 12.77$ (1, 28); $p < 0.01$) between artificial and natural waterbodies, after channel location was statistically accounted for in the mixed model ANOVA. Compared to artificial waterbodies, mean (SD) = 1.18 (±0.40), naturally occurring sites had higher average DBI/site scores, mean (SD) = 2.14 (±1.36) (Figure 2.7). Most artificial sites had relatively similar DBI scores (min = 0.5, max = 1.93, range = 1.43), while natural sites were far more wide-ranging (min = 0.75, max = 4, range = 3.5). The weir site had a higher DBI/site score (1.71) than other naturally occurring sites in river channels, mean (SD) = 1.36 (±0.49).

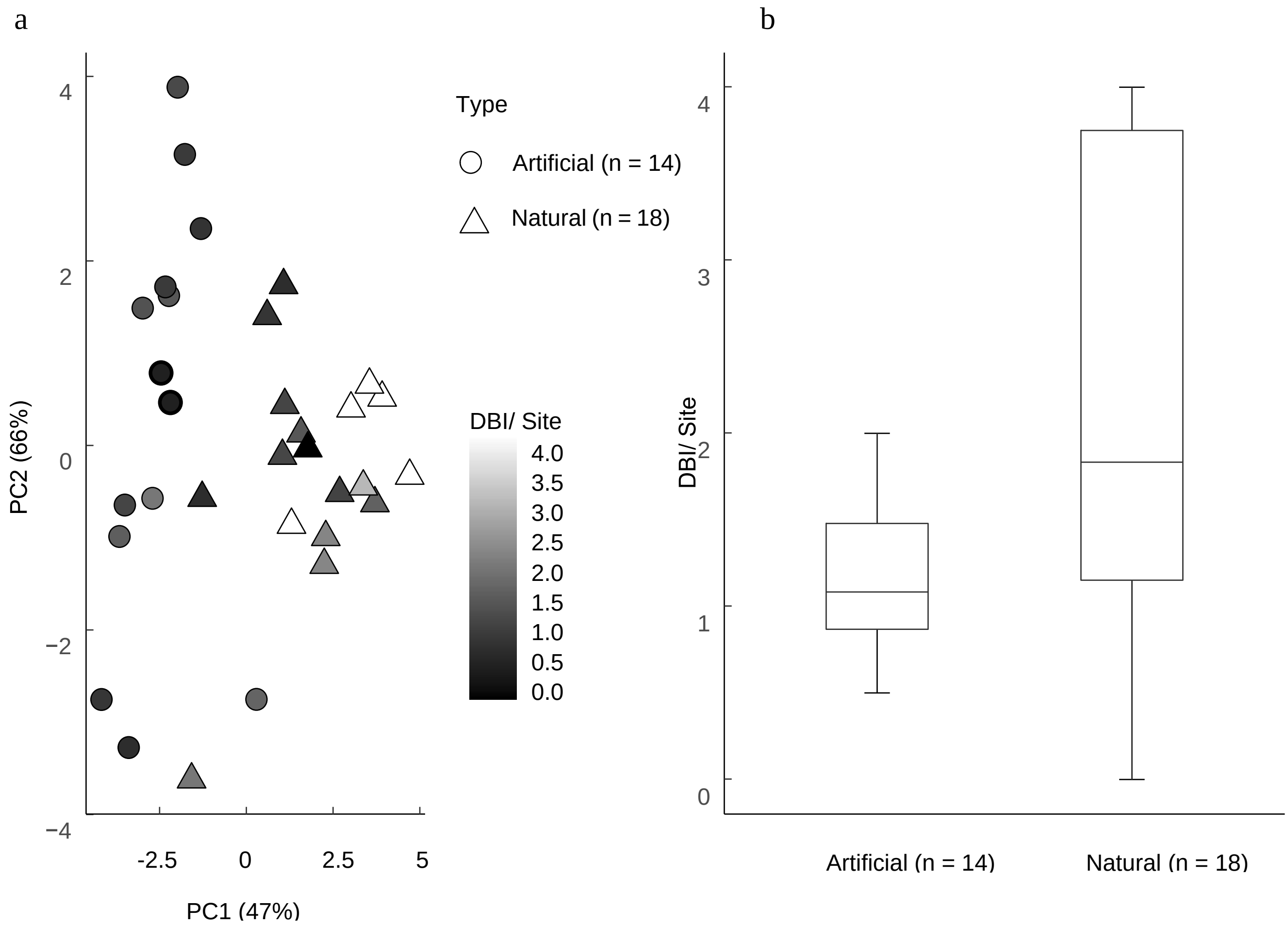

Figure 2.7: a) Principal component (PC) biplot illustrating the relationship between differences in sites according to environmental variables (distance between points), site types (shape) and Dragonfly Biotic Index per Site score (DBI/site) (colour scale). b) Box and whisker plot showing differences (minimum, maximum, mean, first and third quartile) in DBI/site between natural and artificial waterbodies.

Discussion

I found that artificial waterbodies had significant differences in environmental variables, DBI scores, and species diversity, compared to those of natural waterbodies. Even though the assessment techniques accounted for hydrogeomorphic location, these results relate largely to sites within tributary channels. This finding is due to the number of both natural and artificial sites with perennial surface water occurring in high order tributary channels. Such significant differences in environmental variables were expected in tributary channels considering the well-documented impacts of channel modification on forested subtropical intermittent tributary streams (Cantonati et al. 2020; Deacon et al. 2020). Reductions in suitable habitat that result from channel modification, such as invasion of exotic trees, is one of the greatest threats to *Chlorolestes apricans* in the Eastern Cape, South Africa (Samways 1999). In this transitional mosaic, naturally occurring well-forested tributary deposition pools support high scoring, niche specific taxa with high DBI scores. They also provide clean drinking water for grazing animals. In this regard, naturally occurring deposition pools within tributary channels could be considered irreplaceable within a grazing waterscape.

The results indicated that in certain circumstances, excavations out of a channel can also attract relatively high scoring, range limited taxa, like *Orthetrum stemmale*. During periods of low rainfall, depressions constructed outside of a channel are a novel source of perennial water in these rangeland waterscapes. This observation is supported by the fact that during the preliminary site survey, none of the naturally occurring depressions were inundated with water. This complementation to natural waterbodies within a waterscape was also found to be the case in the Cape Fold Ecoregion and in the province of KwaZulu-Natal (Simaika et al. 2016; Deacon et al. 2018; Deacon et al. 2019; Briggs et al. 2019a; Jooste et al. 2020). , These artificial waterbodies contribute to waterscape conservation by providing a refuge for lentic taxa in drought prone or degraded areas (Samways 2020).

The only artificial river deposition pool (weir) that featured in this study is of particular interest as it was uncharacteristic of the other artificial sites found in this study. The weir had similar environmental components to other natural river deposition pools, one of the highest DBI/site scores and high diversity of species present. Additionally, this weir provided refuge for an endemic and endangered damselfly (*Metacnemis valida*). Occupation of *Metacnemis valida* at this weir has been recorded for three years so far (2019 -2021) (iNaturalist 2021). This species requires pools with good water quality and perennial flow. The fact that *Metacnemis valida* occurred in a human-modified habitat (a weir) is particularly motivating. This is a species under severe pressure from invasive alien trees that shade out its natural habitat. It is now known that certain rare endemic species will occupy artificial waterbodies when local environmental conditions, such as drought, are having a severe impact on their natural habitat (Deacon et al. 2019). The fact that *Metacnemis valida* has sufficient behavioural plasticity to colonize artificial habitats like weirs here is encouraging, suggesting that this newly discovered adult habitat preference should be investigated further to determine whether it can complete its life cycle in them.

Conservation recommendations

This study highlights that a regional understanding is fundamental for conservation in agro-ecological waterscapes. The results here suggest that both natural and artificial waterbodies can provide clean drinking water for grazing livestock as well as irreplaceable biological habitat for aquatic biota. However, this is against the background that appropriate hydrogeomorphic conditions are essential for maintaining waterscape integrity.

Natural deposition pools within high order tributary channels are irreplaceable, while artificial waterbodies constructed in tributary channels are harmful to the ecological integrity of the waterscape here. Intense channel modifications for the construction of water storage features should not be considered within this hydrogeomorphic location. If necessary, careful consideration should be taken to mimic waterbodies that occur naturally. Excavations outside of stream channels are good complements to natural depressions within these grazing waterscapes. They support diverse, non-competing taxa, do not interfere with natural waterbody habitat integrity, are manageable, and provide accessible high-quality drinking water for grazing animals. Experimental studies should be considered to determine optimal conditions for favourable waterbody parameters for both conservation and agriculture.

Within river channels, the construction of water level control features, like weirs, need to be carefully considered. On the one hand, this type of structure can provide a manageable and perennial source of water for biota among potentially degraded landscapes (Clifford and Heffernan 2018). On the other hand, it can have downstream hydrological implications, facilitate invasions, and prevent anadromous migrations (Wu et al. 2019). Considering their potential symbiotic relationship in agro-ecological grazing areas of the ECBE, conservation practitioners should look beyond an expected inherently low biotic value of weirs and prescribe weir designs that resemble natural depositions pools. Close attention needs to be paid to maintaining natural flow regimes that maintain connectivity and allow anadromous migrations (Council for Scientific and Industrial Research 2021). For example, nonlinear, folded weirs improve stream connectivity by reducing the variation in flow rate between high and low flow cycles (Erpicum 2014; Ansari et al. 2020). Other weirs facilitate fish migration with customized channels called ‘fishways’ (Yagci 2010). In the Katumba River, Tanzania, weirs are even being used to restore river flow (Elisa et al. 2021).

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Chapter 3

Biotic and abiotic characteristics of waterscape condition among rangelands in the Eastern Coastal Belt Ecoregion

Abstract

Agriculture is a significant driver of environmental impact on freshwater ecosystems globally. However, in some cases agricultural and freshwater ecosystems are mutualistic , promoting dynamic and resilient agro-ecological systems. Contextualising significant environmental variables and biological indicators of healthy and compromised agro-ecological systems is vital to regional conservation planning and restoration efforts. Here, a comparative analysis of environmental variables and dragonfly assemblage composition was conducted between small perennially inundated waterbodies (waterbodies), both natural and artificial, in various hydrogeomorphic forms among livestok grazing areas (rangelands) in the Eastern Coastal Belt Ecoregion, South Africa. Tributary deposition pools had higher Dragonfly Biotic Index Scores per site (DBI/site) when supporting indigenous riparian forest and minimal fine sediment deposition, attracting high scoring species like *Chlorolestes tessellatus*, while excluding other generalist and lentic species. At river deposition pools, relatively high scoring species, like *Crocothemis sanguinolenta*, *Tetrathemis polleni*, *Pseudagrion hageni* and *Chlorolestes tessellatus*, were sensitive to compromised water physio-chemical conditions, diminished structure and composition of riparian vegetation, homogeneity of macrophytes, and deposition of fine grain sediments. Some species were reliable indicators of general habitat quality (*C. sanguinolenta*), riparian habitat (*T. polleni, P. hageni,* and *C. tessellatus*), and successful restoration (when replacing *P. flavescens*). In depressions outside of a stream channel, the presence of a variety of substrates, macrophytes and indigenous bushy riparian vegetation attracted high scoring lentic taxa. Habitat heterogeneity should be considered as a key component of depression restoration in the region. To indicate effectiveness of restoration, low scoring dragonflies: *Africallagma glaucum*, *Lestes plagiatus*, *Pantala flavescens* and *Pseudagrion massaicum* were replaced by a characteristic composition assemblage of higher scoring taxa: *Azuragrion nigidorsum*, *Diplacodes luminans*, *Tramea limbata*, *Anax imperator*, *Crocothemis sanguinolenta*, *Anax ephippiger* and *Orthetrum stemmale*, a benchmark for high-quality habitat in the region.

Keywords: restoration, biological indicators, regenerative agriculture, waterscape integrity

Introduction

Agriculture is a significant driver of environmental impact on freshwater ecosystems via a multitude of complex pathways (Dala-Corte et al. 2016; Chen et al. 2018; Melland et al. 2018). For instance, the intensity and frequency of physical disturbance from livestock on aquatic and riparian environments can facilitate homogenisation of vegetation, structurally, functionally, and compositionally (Bruno et al. 2016), as well as facilitating the colonization of exotic biota (Leitão et al. 2018). Homogenisation of aquatic and riparian vegetation may lead to several environmental changes that reduce hydroperiod, modify biophysical features related to substrate, and alter physio-chemical properties such as temperature and turbidity (Leitão et al. 2018; Cantonati et al. 2020). Manure from livestock also influences water quality through nutrient inputs to the system (Julian et al. 2017; Melland et al. 2018; Evans et al. 2019). Such habitat modifications can directly and/or indirectly alter the assemblage composition of aquatic biota (Albertson et al. 2018; Davis et al. 2018; Granzotti et al. 2018; O'Callaghan et al. 2019) and reduce the efficiency of the aquatic system in providing valuable ecosystem services (Datry et al. 2018; Pogue et al. 2018; Dudgeon 2019).

Small perennially inundated waterbodies (< 2 ha), here referred to as waterbodies, occur in a variety of hydrogeomorphic forms, both naturally and constructed (artificial) (Hill et al. 2018), and are a common feature of livestock rangelands. A group of waterbodies in the same location constitutes a waterscape, providing drinking water for livestock and collectively contributing to the conservation of biodiversity and ecosystem resilience (Simaika et al. 2016; Deacon et al. 2018; Samways et al. 2020; Zamora-Marín et al. 2021). 'Ecosystem health' is a seminal term used in conservation ecology to describe the state of a system relative to a desired reference condition or management objective (Schaeffer et al. 1988; Rapport 1989). The principles of ecosystem health describe measures of sustainability and resilience, as well as the condition of a habitat relative to its ability to supply ecosystem services (O'Brien et al. 2016). Approaches used to define an ecosystem's state of health often involve identifying environmental indicators (e.g., algal blooms to signify eutrophication), measuring biological diversity, studying ecological interactions, assessing shifts in composition of biological assemblages, analysing biological indices, and defining a regional or system-specific benchmark condition (Jackson et al. 2016).

Dragonflies (Odonata), including both damselflies (Zygoptera) and dragonflies (Anisoptera) (both groups of which are here collectively called 'dragonflies'), are excellent indicators of habitat quality, as they are sensitive to local environmental changes, well studied taxonomically, highly visible, widely distributed, and have life cycles with both aquatic (larval) and terrestrial (adult) stages (Simaika and Samways 2009; Simaika and Samways 2011; Samways and Simaika 2016). Adults are highly mobile, and respond to changes in a landscape, whether improving or deteriorating, shaping resident assemblage composition (Simaika and Samways 2009; Simaika et al. 2016; Kietzka et al. 2017; Deacon et al. 2020).

Studies in South Africa have shown that riparian and aquatic vegetation diversity and structure are important drivers of habitat heterogeneity and assemblage composition in dragonflies (Briggs et al. 2019; Deacon et al. 2019). In both the Cape Floristic Region (CFR) and the Maputuland-Pondoland-Albany biodiversity hotspot (MPA) (Myers 2003), dragonflies are highly responsive to water physio-chemistry and hydrology (Kietzka et al. 2017; Deacon et al. 2018; Deacon et al. 2020; Jooste et al. 2020). Studies in the Northeast of South Africa have shown that dragonflies are also good indicators of riparian restoration, as they respond well to riparian habitat rehabilitation and clearing of alien vegetation (Magoba and Samways 2010; Modiba et al. 2017).

Hydrogeomorphology and hydrological regime drive functional connectivity, habitat structural diversity, and spatial arrangement within a waterscape (Stanley et al. 1997; Arthington et al. 2006, Ollis et al. 2015; Boulton et al 2017). Deposition pools in intermittent streams and rivers receive concentrated water inflow and outflow through drainage channels (Ollis et al. 2013). Low flow pools are abundant and connected by visible water inflow and outflow (Boulton et al. 2017). During prolonged dry periods however, they become isolated from visible flow and have many similarities to lentic waterbodies (Boulton et al. 2017). These small waterbodies are well vegetated and compositionally diverse, and often occupied by endemic aquatic biota (Bird et al. 2019; Bonada et al. 2020; Magand et al. 2020). Here, water quality is influenced by local and upstream activity and extreme conditions that are harmful to biodiversity (Darwall et al. 2009). Substrate composition in these pools is governed by the hydrological regime and organic matter input. High flow velocities transport larger grain size and deposit substrate types like boulders and cobbles (Jaeger et al. 2017).

Deposition pools located in smaller channels, like small tributary streams, have lower flow velocities and greater amounts of riparian cover (Boulton et al. 2017). The riparian vegetation provides organic matter and lowers flow velocity, typically supporting fine grain sediments (pebble, gravel, sand) (Lupon et al. 2016; Jaeger et al. 2017; Trimmel et al. 2018). Pools that have exceptionally low, or no flow, accumulate organic matter and often comprising a muddy benthic environment (Hauer et al. 2018). Also, reducing the amount of exposed impermeable substrate like bedrock can impact on the formation of small deposition pools (Jaeger et al. 2017; Hauer et al. 2018).

In contrast, depressions that occur outside of channels receive diffuse surface water and groundwater that accumulate due to the impermeable underlying layer and closed elevation contour (Ollis et al. 2013; Ollis et al. 2015). These vernal pools dry out when there are prolonged periods of no or low rainfall and are vulnerable to disturbance from agricultural activity (Samways et al. 2020).

Understanding waterbody biological diversity helps maximise waterscape conservation (Hill et al. 2018). In South Africa, there is much information documenting the relationship between dragonfly composition assemblages and agricultural land use practices. However, little is known about this relationship in the Eastern Coastal Belt Ecoregion (ECBE), where we need to gain a better regional understanding of the extent to which dragonfly assemblages respond to changes in waterbody environmental variables. Achieving this is the first step toward guiding both conservation planning, restoration efforts, and engaging farmers in actions relating to the maintenance of healthy agro-ecological systems.

The aim of this study is to examine environmental drivers of dragonfly assemblage composition to ascertain regionally significant characteristics of near-natural and modified waterbodies, within livestock grazing areas of the ECBE. specifically addressing the following questions:

a) What is the extent of correlation between Dragonfly Biotic Index site scores (DBI/site, see below) and sets of environmental variables among waterbodies within rangelands around Chintsa Bay, ECBE, South Africa?

b) Which dragonflies are responsible for high and low DBI/site scores in the area?

By drawing inferences about environmental components of waterbody integrity, these questions will facilitate better management of rangelands waterscape while maintaining high levels of local dragonfly diversity.

Materials and methods

Study sites and survey methods

I used the same 32 sites (11 within river channels, 14 within tributary channels and seven outside of any channel) where dragonfly and environmental variables were sampled in chapter 2 of this thesis, to make inferences about environmental components of waterbody integrity. A detailed description of the study area and the procedure used to select sites are provided in chapter 2. A total of 32 environmental variables were measured at each site. A detailed description of the sampling methods and equipment used can also be found in chapter 2. Dragonflies were surveyed at each site following a procedure adapted from the Dragonfly Biotic Index (DBI) manual (Samways and Simaika 2016). A detailed description of this procedure can be found in chapter 2. Each dragonfly species was assigned a DBI score ranging from 0 to 9, based on its geographic range, threat status (according to the IUCN Red List), and sensitivity to habitat change. The DBI scores of each species present at a site were added up to provide a total DBI score at each site. This DBI total score was divided by total species richness to give a DBI/site score. The DBI/site score assesses ecosystem integrity and enables a comparison of the focal ecosystems' relative ecological state.

Data analyses

Visualizing environmental components of sites within hydrogeomorphic location

To visualize differences in environmental parameters between waterbodies within their hydrogeomorphic location, all sets of environmental variables were analysed through separate Principal Component Biplots (PC biplot) (Gower and Hand 1996) according to the sites hydrogeomorphic location (deposition pool in tributary channel, deposition pool in river channel or depression/excavation outside of a channel).

Environmental drivers of waterbody DBI/site scores

Spearman's rank correlation coefficients (r_s) (Sedgwick 2014) were used to assess the extent of complementarity between DBI/site scores and measured environmental parameters within site hydrogeomorphic location. This test was chosen because it is the appropriate correlation test for non-parametric data. Environmental variables that had significant ($p < 0.05$; CI: 95%) relationships with DBI/site scores were tabulated (Appendices, table 3.1). To visualize the relationship between DBI/site score and environmental variables, a correlation biplot was constructed using environmental variables that had a moderate to strong ($-0.4 > r_s > 0.4$) correlation with DBI/site score.

Species representative of differences in DBI/site score

To determine the extent of relationship between DBI/site scores and presence or absence of potential dragonfly indicator species, species presence/absence was compared to DBI/site scores using a biserial correlation coefficient (r_{pb}) (Kornbrot 2005). Species with a moderate to strong ($-0.4 > r_{pb} > 0.4$) relationship with DBI/site score were plotted comparatively on individual boxplots. An Analysis of Variance (ANOVA) was used to assess whether there was significant variation between dragonfly presence and absence and DBI/site scores. Prior to the ANOVA, DBI/site scores were observed for trends in normality using a Shapiro-Wilk test (Shapiro and Wilk 1965). Environmental variables that deviated from a normal distribution ($p > 0.05$; CI: 95%), were assessed using a non-parametric Mann–Whitney U-test (Wilcoxon 1946; Mann and Whitney 1947). A Levene's test (Levene 1960) was then conducted to assess the equality of variances among measured parameters.

Software used

All analyses were conducted using R statistical software packages: '*base R*' (R core team 2013) and '*ggplot*2' (Wickham 2011).

Results

Environmental components according to waterbody hydrogeomorphic location

Sites within tributary channels separated into two distinct groups within multivariate habitat space (Figure 3.1a), indicating consistent differences in environmental parameters. One group of sites was characterised by larger water surface area, mean (SD) = 2595.69 m^3 (±3591.73), warmer water, temperature mean (SD) = 28.38 C° (±4.42) with a muddy substrate, mean (SD) = 44.76% (±39.78). These sites had dominant herbaceous and aquatic vegetative percentage cover, comprised of mostly Juncaceae spp. mean (SD) = 6.04% (±10.13), Cyperaceae spp. mean (SD) = 7.61% (±12.69) and Poaceae spp. mean (SD) = 11.14% (±8.97).

The riparian vegetation was short (0-1 m) in stature, mean (SD) = 24.29% (±27.31) offering less canopy cover, mean (SD) = 42.86% (±39.55). In contrast, the other group of sites were generally smaller with a substantial percentage cover of riparian forest, offering almost complete canopy cover. These waterbodies usually had a variety of larger grain sedimentary deposits, pebble mean (SD) = 2.38% (±3.31), gravel mean (SD) = 5.71% (±8.61), as well as bedrock, mean (SD) = 27.62% (±30.48). They contained little to no aquatic vegetation, and were characterised by a small but diverse array of marginal herbaceous macrophyte percentage cover, geophyte mean (SD) = 2.00% (±2.44), herbs and forbs mean (SD) = 5.46% (±5.49), Eriocaulaceae spp. mean (SD) = 2.00% (±2.45), and absence of Typhaceae spp. and Juncaceae spp.

River deposition-pool sites were more weakly grouped than tributary sites. However, polarities are evident in sites according to environmental variables in multivariate habitat space (Figure 3.1b). Major differences in environmental variables between sites is apparent among water physio- chemical properties, temperature mean (SD) = 26.81 C° (±3.21), pH mean (SD) = 7.15 (±0.29), electrical conductivity (EC) mean (SD) = 570.08 µm (±140.63) and total dissolved solids (TDS) mean (SD) = 282.41 ppm (±69.95). Sites that were warmer with relatively high concentrations of TDS and EC, were also characterised by higher percentage cover of algae, mean (SD) = 5.00% (±13.42) and herbaceous vegetation like Typhaceae spp. mean (SD) = 0.91% (±2.20) and Poaceae spp. mean (SD) = 7.72% (±7.53). These sites were also characterised by short (0-1 m) and medium (0-4 m) stature riparian vegetation, 0-1 m mean (SD) = 24.09% (±21.88) and 1-4 m mean (SD) = 16.82% (±19.78), with a fairly high percentage cover of exotic species, mean (SD) = 24.56% (±21.73). In contrast, were sites characterised by a riparian forest and thicket mosaic, 4-7 m mean (SD) = 23.18% (±19.91) and 7-10 m mean (SD) = 24.09% (±21.42), that were generally cooler with a lower EC and TDS. These sites also had a diverse composition of marginal herbaceous vegetation with no single dominating group, which included geophytes, mean (SD) =5.23% (±6.16), Eriocaulaceae spp. mean (SD) = 3.18% (±2.52), Cyperaceae spp. mean (SD) = 9.77% (±9.38) and herbs/forbs, mean (SD) = 5.68% (±5.93).

Depression sites were not distinctly grouped in the multivariate habitat space (Figure 3.1c). The ordination biplot indicates that while there are polarities in sites in relation to environmental components, these differences are not consistent between samples. Depression sites had little canopy cover, mean (SD) = 5.71% (±8.10) but high percentage cover of short (0-1 m) riparian vegetation, mean (SD) = 77.86% (±16.55). Some sites had a dispersed dense woody/thicket component, 4-7 m mean (SD) = 4.28% (±7.31) around them, with exotic species and without, mean (SD) = 7.14% (±8.09). Most sites were dominated by aquatic and herbaceous marginal vegetation. However, the assemblage composition and percentage cover of dominant groups differed among sites: free floating mean (SD) = 4.28% (±9.32), floating rooted mean (SD) = 17.14% (±23.25), submerged mean (SD) = 25.00% (±41.43), algae mean (SD) = 9.28% (±18.35), Juncaceae spp. mean (SD) = 11.43% (±13.14), Typhaceae spp. mean (SD) = 1.43% (±2.44), Poaceae spp. mean (SD) = 22.14% (±16.80), Cyperaceae spp. mean (SD) = 7.85% (±7.55), and herb/forb mean (SD) = 8.57% (±7.48). The benthic environment was composed of fine-grained sediments, but differed in proportions of mud, mean (SD) = 76.19% (±24.60) and loam, mean (SD)=17.14% (±23.05).

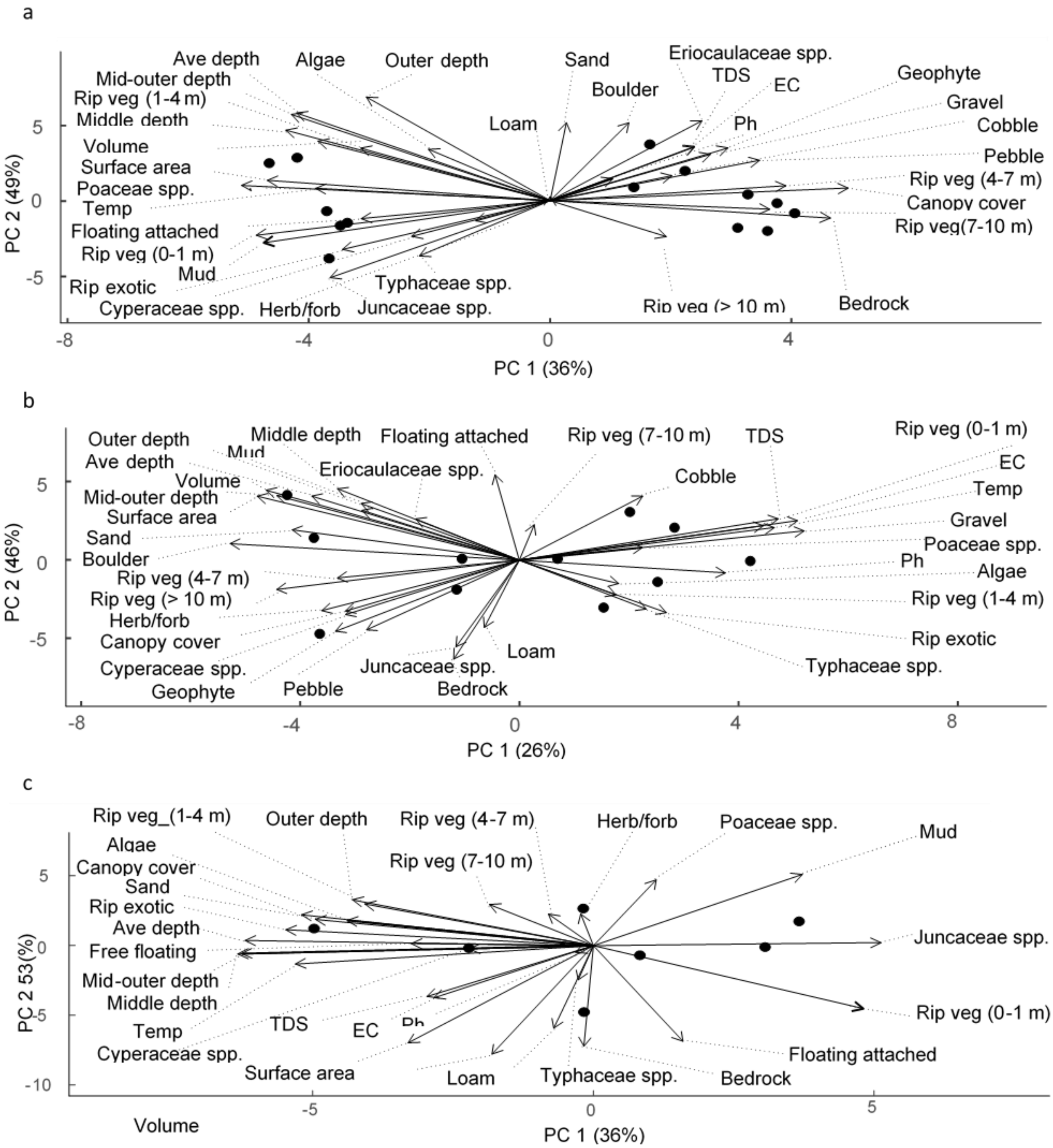

Figure 3.1: Principal Component (PC) Analysis biplot summarizing environmental conditions in a) tributary deposition pools, b) river deposition pools and c) out of channel depressions. The length and direction of vectors (solid black lines) indicate the relationship between environmental variables, as well as the strength of influence of each environmental variable on the variation in overall environmental conditions among sampling sites. Rip veg = riparian vegetation; EC = electrical conductivity; TDS = total dissolved solids; Temp = water temperature; Ave = average

Complementarity of dragonflies and environmental parameters with DBI/site score

In tributary deposition pools, 18 environmental variables had a moderate to strong ($-0.40 > r_s > 0.40$) correlations with DBI/site score (Figure 3.2a), 14 of them were statistically significant ($p > 0.05$; CI: 95%; Table 3.1, Appendix 1). Water temperature ($r_s = -0.65$), water surface area ($r_s = -0.69$), water volume ($r_s = -0.69$), and water average depth ($r_s = -0.58$) were all negatively correlated with DBI/site scores. Additionally, the percentage cover of herbaceous macrophytes, Poaceae spp. ($r_s = -0.61$) and Typhaceae spp. ($r_s = -0.51$), as well as algae ($r_s = -0.58$) were also negatively correlated with DBI/site score. However, there were positive correlations between DBI/site scores and marginal geophyte percentage cover ($r_s = 0.47$).

There were negative correlations in the riparian environment between DBI/site score and the amount of exotic ($r_s = -0.74$) and short (0-1 m) riparian vegetation cover ($r_s = -0.61$), which contrasted with strong positive correlations between DBI/site score and tall (7-10 m) riparian vegetation ($r_s = 0.54$) as well as with the associated high percentage of canopy cover ($r_s = 0.73$). Amount of gravel ($r_s = 0.40$) and bedrock ($r_s = 0.58$) comprising the benthic environment had positive correlations with DBI/site score. This contrasted with the percentage cover of mud ($r_s = -0.53$), which had a moderate negative correlation with DBI/site score.

In tributaries, nine dragonfly species showed a moderate to strong ($-0.40 > r_{pb} > 0.40$) correlation with DBI/site score (Figure 3.2b). Presence of a single damselfly species, *Chlorolestes tessellatus* (DBI = 4.00, $r_{bp} = 0.86$), only occurred at sites with relatively high DBI/site scores (DBI/site = 2.00 - 4.00). *Crocothemis erythraea* (DBI = 0.00, $r_{bp} = -0.80$), *Anax imperator* (DBI = 1.00, $r_{bp} = -0.71$), *Ceriagrion glabrum* (DBI = 0.00, $r_{bp} = -0.54$), *Ischnura senegalensis* (DBI = 0.00, $r_{bp} = -0.71$), *Lestes tridens* (DBI = 3.00, $r_{bp} = -0.59$), *Pantala flavescense* (DBI = 0.00, $r_{bp} = -0.51$) and *Trithemis arteriosa* (DBI = 0.00, $r_{bp} = -0.56$) all occurred consistently at relatively low scoring sites (DBI/site score = 0.75-1.00).

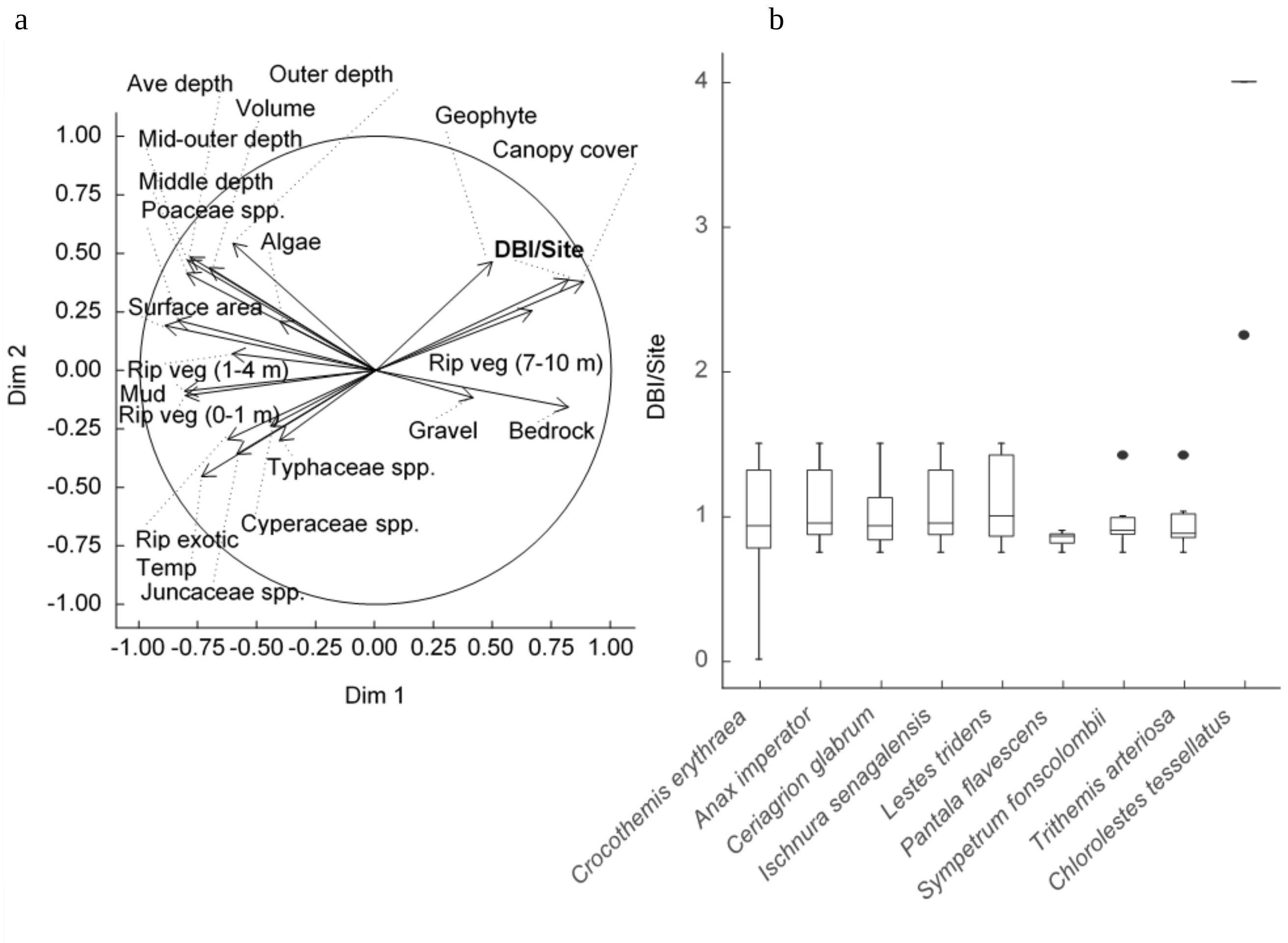

Figure 3.2: Tributary channel deposition pools a) correlation biplot showing the correlation between DBI/site score and environmental variables measured at each site. The length and direction of vectors (solid black lines) indicate the strength and relationship (positive or negative) between each variable, and b) comparative box and whisker plots illustrating the dragonfly species responsible for high and low DBI/site scores at each site, as well as the minimum, maximum, average, first and third quartile DBI/site score that each species was present or absent at. Dim = Dimension; Rip veg = riparian vegetation; Ave = average; DBI/site = Dragonfly Biotic Index Site score

In river deposition pools, 18 environmental variables shared a moderate to strong ($-0.40 > r_s > 0.40$) correlation with DBI/site score (Figure 3.3a), eight of them were statistically significant ($p > 0.05$; CI: 95%; Table 3.1, Appendix 1). Sites that were larger (surface area $r_s = 0.68$, volume $r_s = 0.55$) were positively related to DBI/site score. Water physio-chemical parameters were all inversely related to DBI/site score (Temp $r_s = -0.65$, TDS $r_s = -0.72$, EC $r_s = -0.77$, pH $r_s=-0.48$). Similarly, negatively correlated with DBI/site scores were amount of low stature (0-1 m) ($r_s = -0.41$) and exotic riparian vegetation ($r_s = -0.40$) present at a site. In contrast, DBI/site scores were positively correlated with amount of tall (4-7 m) riparian vegetation offering canopy cover in places ($r_s = 0.59$). Percentage cover of Eriocaulaceae spp. ($r_s = 0.66$) and herbs/forbs ($r_s = 0.49$), were positively correlated with DBI/site score. The percentage cover of sand ($r_s = 0.83$) and boulder ($r_s = 0.63$) both had a positive relationship with DBI/site score, while the amount of gravel ($r_s = -0.58$) was inversely related to DBI/site score.

In river deposition pools, five dragonfly species had a moderate to strong ($-0.40 > r_{bp} > 0.40$) correlation with DBI/site score (Figure 3.3b). *Crocothemis sanguinolenta (*DBI = 3.00, $r_{bp} = 0.66$*)* consistently occurred at sites with significantly higher DBI/site scores (DBI/site = 1.71-2.00). *Pantala flavecsens* (DBI = 0.00, $r_{bp} = -0.66$) was consistently absent from high scoring sites and was only present at low scoring sites (DBI/site = 0.75-1.71). Although not statistically significant ($p > 0.05$; CI: 95%), *Pseudagrion hageni* (DBI = 5.00, $r_{bp} = 0.58$) only occurred at two high scoring sites (DBI/site scores = 1.66 and 2.00). *Tetrathemis polleni* (DBI = 3.00, $r_{bp} = 0.57$) and *Chlorolestes tessellatus* (DBI = 4.00, $r_{bp} = 0.48$) were absent from the lowest scoring sites, although present at sites with relatively higher DBI/site scores (DBI/site = 1.14-2.00).

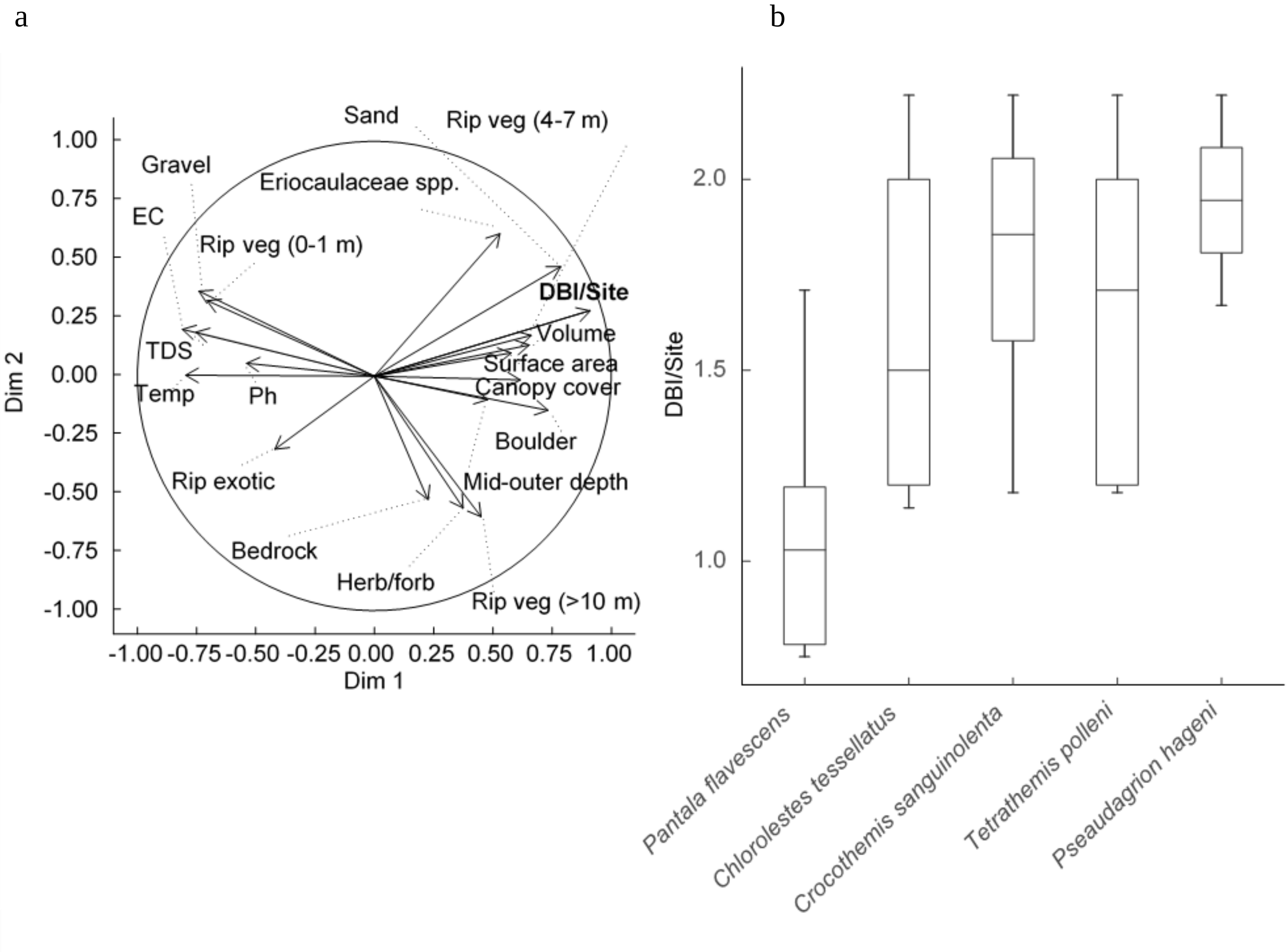

Figure 3.3: River channel deposition pools a) correlation biplot showing the correlation between DBI/site score and environmental variables measured at each site. The length and direction of vectors (solid black lines) indicate the strength and relationship (positive or negative) between each variable, and b) comparative box and whisker plot illustrating the dragonfly species responsible for high and low DBI/site scores at each site, as well as the minimum, maximum, average, first and third quartile DBI/site score that each species was present or absent at. Dim = Dimension; Rip veg = riparian vegetation; EC = electrical conductivity; TDS = total dissolved solids; Temp = water temperature; Ave = average; DBI/site = Dragonfly Biotic Index Site score

In the case of depressions outside of a channel, eight environmental variables shared a moderate (-0.40 > r_s > 0.40) correlation with the DBI/site score (Figure 3.4a), two of them were statistically significant (*p* > 0.05; CI: 95%; Table 3.1, Appendix 1). Water body size (volume r_s = 0.43 and surface area r_s = 0.67) was positively correlated with DBI/site score. Likewise, the amount and type of aquatic macrophytes (free floating r_s = 0.54, floating attached r_s = 0.42) and herbaceous macrophytes (Cyperaceae spp. r_s = 0.61 and Poaceae spp. r_s = 0.35), were positively correlated with DBI/site score. The percentage cover of algae had a negative correlation (r_s = -0.39) with DBI/site score. In the riparian zone, amount of bushy (1-4 m) riparian vegetation, shared a positive relationship (r_s = 0.43) with DBI/site score. Amount of mud in the substrate was significantly (*p* < 0.05; CI: 95%) negatively correlated with DBI/site score (r_s = -0.92). This was in contrast to sites with a larger composition of loam (r_s = 0.86), and in some cases, bedrock (r_s = 0.41) in the substrate.

In depressions, 17 dragonfly species shared a moderate to strong correlation (-0.40 > r_{bp} > 0.40) with DBI/site score. *Pantala flavescens* (DBI = 0.00, r_{bp} = -0.52) and *Pseudagrion massaicum* (DBI = 1.00, r_{bp} = -0.52) were only seen at the two lowest scoring sites (DBI/site score = 0.50). *Africallagma glaucum* (DBI = 1.00, r_{bp} = -0.49) and *Lestes plagiatus* (DBI = 2.00, r_{bp} = -0.49) were also only recorded at low scoring sites (DBI/site score = 0.00-1.00) and were negatively correlated with DBI/site score. *Ischnura senegalensis* (DBI = 0.00, r_{bp} = 0.52) occurred at all sites (DBI/site = 0.50-2.00) and *Sympetrum fonscolombii* (DBI = 0.00, r_{bp} = -0.55) occurred at all but the top scoring sites (DBI/site = 0.5-1.6). *Diplacodes luminans* (DBI = 3.00, r_{bp} = 0.80), *Lestes tridens* (DBI = 3.00, r_{bp} = 0.72), *Anax imperator* (DBI = 1.00, r_{bp} = 0.76) and *Azuragrion nigridorsum* (DBI = 3.00, r_{bp} = 0.8) were positively correlated with DBI/sites scores and occurred at sites with scores between 1.00 and 2.00. *Crocothemis sanguinolenta* (DBI = 3.00, r_{bp} = 0.82), *Anax ephippiger* (DBI = 3.00, r_{bp} = 0.82), *Tramea limbata* (DBI = 0.00, r_{bp} = 0.8) and *Orthetrum stemmale* (DBI = 4.00, r_{bp} = 0.82) were only present at high scoring sites (DBI/site = 1.56-2.00). *Anax speratus* (DBI = 2.00, r_{bp} = 0.69), *Palpopleura lucia* (DBI = 2.00, r_{bp} = 0.69) and *Pseaudagrion hageni* (DBI = 5.00, r_{bp} = 0.69) were only seen once, at the highest scoring site (DBI/site = 2.00).

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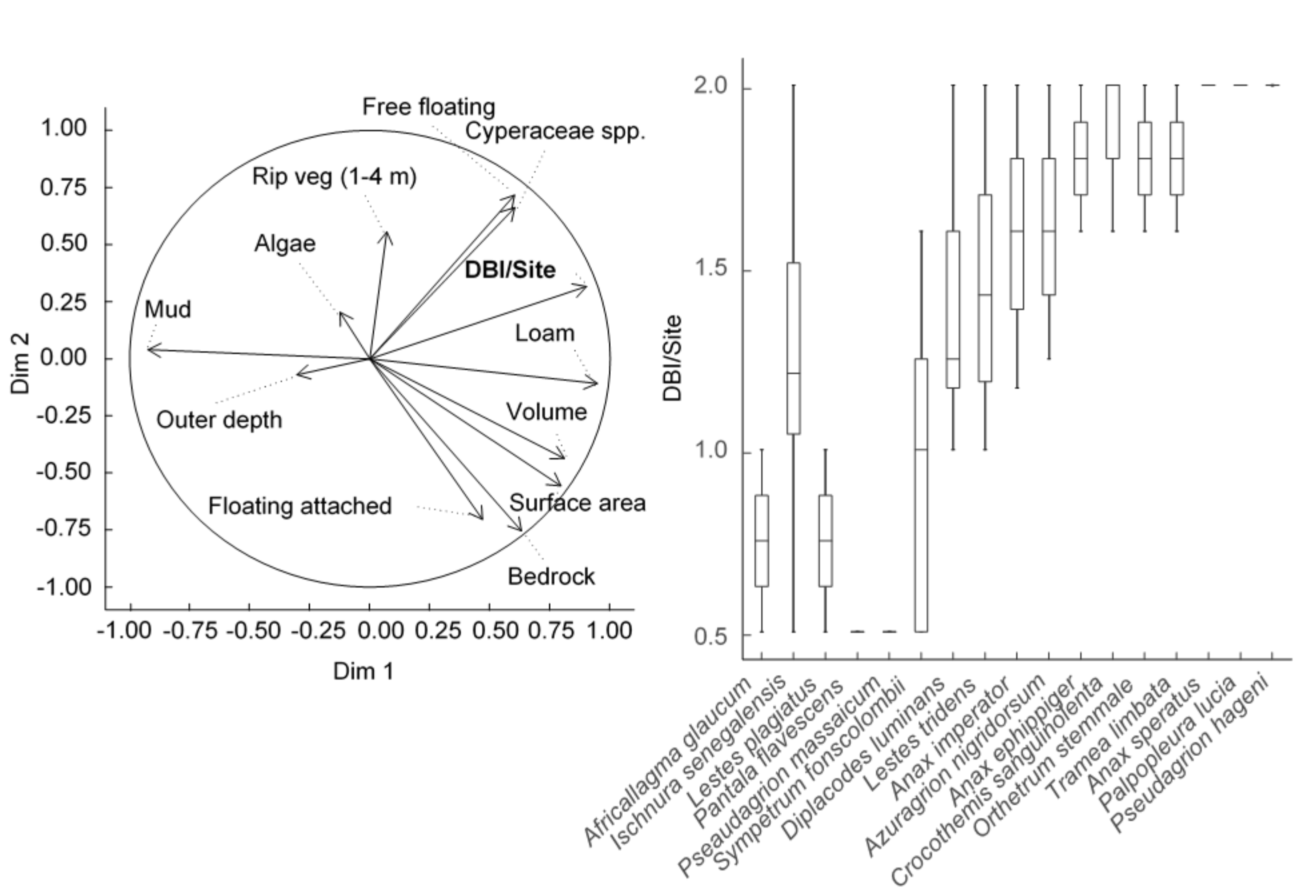

Figure 3.4: Out of channel depression a) correlation biplot showing the correlation between DBI/site score and environmental variables measured at each site. The length and direction of vectors (solid black lines) indicate the strength and relationship (positive or negative) between each variable, and b) comparative box and whisker plot illustrating the dragonfly species responsible for high and low DBI/site scores at each site, as well as the minimum, maximum, average, first and third quartile DBI/site score that each species was present or absent at. Dim = dimension; Rip veg = riparian vegetation; DBI/site = Dragonfly Biotic Index Site score

Discussion

At tributary sites, consistent polarities in groups of environmental variables and DBI/site scores were due to channel modification. Waterbodies within tributary channels had higher scores when supporting indigenous riparian forest and minimal fine sediment deposition, attracting high scoring species like *Chlorolestes tessellatus*, while excluding other generalist and lentic species. This concords with other results, both in South Africa and elsewhere, where channel modification reduces water flow, increases pool water volume, and traps sediment, thereby altering available habitat for sensitive species (de Oliveira-Junior et al. 2017; Rivers-Moore et al. 2018; Borges et al. 2021).

At river deposition pool sites, dragonflies were sensitive to impacts related to both catchment characteristics and magnitude of in-stream disturbance. The DBI/site scores were negatively correlated with poor water physio- chemical conditions, poor structure and composition of riparian vegetation, homogeneity of macrophytes, and deposition of fine grain sediments, seemingly due to a combination of both upstream and local livestock activity affecting habitat quality. These results were expected, and like those in the Cape Fold Ecoregion that show dragonflies respond to in-stream characteristics resulting from prolonged and high magnitudes of disturbance (Kietzka et al. 2018; Deacon et al. 2020). These disturbances include impact from invasive alien vegetation, lack of suitably structured macrophyte and riparian vegetation, as well as accumulation of fine sediment (Kietzka et al. 2017; Modiba et al. 2017; Janssen et al. 2018; Briggs et al. 2019; Deacon et al. 2020; O'Malley et al. 2020).

Some dragonfly species were good indicators of these shifts in habitat condition. *Crocothemis sanguinolenta* was sensitive to impacts in stream condition and occurred consistently at sites with relatively high DBI/site scores. In Addo Elephant National Park, *C. sanguinolenta* occurs in streams with perennial flow, emergent vegetation, and areas with large particle substrate deposition (Dijkstra 2021). *Tetrathemis polleni, Pseudagrion hageni,* and *Chlorolestes tessellatus* were absent from low-scoring deposition pools, but characteristic of sites with relatively high DBI/site scores. All of these three species are associated with streams that have quality structure and composition of riparian forest and are sensitive to alien tree invasion (Samways and Simaika 2016).

In contrast, *Pantala flavescens* appeared at many different sites, but was absent from sites with the highest DBI/sites scores. The species is a strong flyer and breeds in shallow, warm, grassy, and often temporary pools in open areas (Samways and Simaika 2016). In this region of the ECBE, the occurrence of *P. flavescens* can indicate decline of deposition pool habitat quality, specifically relating to the riparian and hydrological environment.

Artificial waterbodies outside of a stream channel and perennially inundated with water are valuable habitat for lentic species in drought-prone South Africa (Deacon et al. 2019). This is the case here for the ECBE, if certain environmental variables are present. These include amount and variety of substrates, presence of macrophytes, and presence of indigenous bushy (1-4 m) riparian vegetation. Overall, these variables together highlight the importance of quality habitat heterogeneity in encouraging an assemblage of high-scoring dragonfly species. These findings also support those in the CFR and KwaZulu-Natal, where high-quality habitat heterogeneity is fundamental at both individual waterbody and waterscape levels (Briggs et al. 2019; Jooste et al. 2020; Samways et al. 2020).

Some dragonfly species were good indicators of high- and low-quality habitat heterogeneity in these artificial waterbodies. *Africallagma glaucum, Lestes plagiatus, Pantala flavescens* and *Pseudagrion massaicum* were characteristic species at sites with low DBI/site scores. In contrast, *Azuragrion nigidorsum, Diplacodes luminans, Tramea limbata, Anax imperator, Crocothemis sanguinolenta, Anax ephippiger* and *Orthetrum stemmale* were associated with sites with high DBI/site scores. Two species, *Sympetrum fonscolombii* and *Ischnura senegalensis*, were present at a wide range of artificial waterbodies. Although *I. senegalensis* had a positive relationship with DBI/site score, it is a lentic generalist in the region. *Sympetrum fonscolombii* had a negative correlation with DBI/site score and was absent from the highest scoring sites.

Management recommendations

Conservation efforts should aim to represent natural waterbodies. Overall, the focus should be on reducing surface area/perimeter ratio, increasing canopy cover, improving macrophyte cover and maintaining flow regimes that will allow deposition of appropriate sediments. To validate success of such conservation efforts, various species that were characteristic of good conditions can be used. Firstly, presence of *C. sanguinolenta* is a reliable indicator of overall habitat condition of river deposition pools in the region. In turn, presence of *Tetrathemis polleni*, *Pseudagrion hageni*, and *Chlorolestes tessellatus* at river deposition pools indicates relatively good quality riparian habitat in the region. Consequently, replacement of *P. flavescens* by species such as *T. polleni*, *P. hageni* and *C. tessellatus* indicates good stream restoration in the region, at least once riparian vegetation cover has established.

In depressions outside of a channel, where a DBI/site score indicates poor quality habitat, farmers and other land stewards should improve habitat heterogeneity as a key component of waterbody conservation. To validate effectiveness of conservation, there are two groups to consider: 1) *Africallagma glaucum*, *Lestes plagiatus, Pantala flavescens* and *Pseudagrion massaicum*, which are characteristic of sites with low DBI/site scores, and 2) in contrast, *Azuragrion nigidorsum, Diplacodes luminans*, *Tramea limbata*, *Anax imperator*, *Crocothemis sanguinolenta*, *Anax ephippiger* and *Orthetrum stemmale* are characteristic of high-quality sites, i.e., those with high DBI/site scores. As these two groups of species did not overlap, the latter species group is a benchmark for high-quality habitat in the region. Also, absence of *S. fonscolombii* from sites represents certain habitat qualities that are required to attract high scoring taxa, indicating sites that are recovering well.

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Appendices

Table 3.1: environmental variables that show a significant (p < 0.05; CI: 95%) correlation with Dragonfly Biotic Index site score among perennially inundated waterbodies sampled around Chintsa Bay, South Africa (2020)

	Average	SD	r_s
Tributary			
Temp (°C)	28.38	4.42	-0.65
Surface area (m^3)	2595.69	3591.73	-0.69
Volume (m^3)	191848.25	353574.24	-0.69
Average depth (cm)	41.37	35.17	-0.58
Average outer depth (cm)	22.64	19.42	-0.52
Average mid-outer depth (cm)	48.76	40.99	-0.61
Average middle depth (cm)	64.05	61.46	-0.73
Poaceae spp. (%)	11.14	8.97	-0.61
Canopy cover (%)	42.86	39.55	0.73
Algae (%)	2.18	5.91	-0.58
Riparian vegetation (0-1 m) (%)	24.29	27.31	-0.61
Riparian vegetation (7-10 m) (%)	21.79	23.66	0.54
Exotic riparian (%)	12.50	20.45	-0.74
Mud (%)	44.76	39.78	-0.53
River			
Temp (C°)	26.82	3.21	-0.65
Total dissolved solids (ppm)	282.41	69.95	-0.72
Electrical conductivity (µm)	570.08	140.63	-0.77
Surface area (m^3)	2925.59	3216.26	0.68
Erioucaulaceae spp. (%)	3.18	2.52	0.66
Riparian vegetation (4-7 m) (%)	23.18	19.91	0.63
Sand (%)	4.24	6.16	0.83
Boulder (%)	3.64	4.58	0.63
Depression			
Mud (%)	76.19	24.60	-0.92

	Average	SD	r_s
Loam (%)	17.14	23.05	0.86

SD = Standard Deviation; r_s = Spearman correlation coefficient.

Chapter 4

General discussion

A system-specific approach for management of healthy agroecological grazing systems

Livestock agriculture is the largest land use sector globally (Herrero and Thornton 2013). It has an estimated asset value of more than US$1.4 trillion and employs more than 1.3 billion people (Thornton 2010). The livestock industry is also a major contributor to global environmental impacts and has considerable influence on freshwater ecosystem functioning and health. Currently, one third of all freshwater passes through agricultural land (Albert et al. 2021). Eight percent of the global fresh water supply is used for pasture irrigation (Beede 2012), with only 1% used to nourish animals (Doreau et al. 2012). A major contributing factor to this ancillary water usage in intensive livestock production is where water is needed indirectly to raise animals in much larger quantities (Albert et al. 2021).

If agricultural practices continue on this path, socio-economic advances including human, livestock and economic growth will continue to drive an ever-expanding freshwater footprint (Hitchman et al. 2018; Destouni and Jarsjö 2018; Albert et al. 2021). In some scenarios, productive agriculture and healthy ecosystems are integrated, forming a sustainable agroecological system (Young et al. 2018). To address Millennium Development Goals (United Nations 2016) associated with freshwater conservation and sustainable agriculture (such as zero hunger, no poverty, clean water and sanitation, life on land, life below water, climate action and decent work and economic growth), it is imperative that we identify appropriate scenarios for the integration of livestock agriculture and freshwater conservation.

Ruminant livestock in low input production systems are usually raised on rangeland, in continuous grazing systems with minimum external input (Tada et al. 2012; Marandure et al. 2018). In large, naturally occurring and productive subtropical grazing areas, like the Savanna Biome, ruminant livestock act similarly to other naturally occurring megaherbivores, playing an important role in stabilizing the ecosystem, often operating within the conventions of sustainable livestock production (Marandure et al. 2018). Studies globally have shown that with careful management, raising ruminant livestock in these scenarios can be an important driver for necessary ecosystem functions like sequestration of carbon and other nutrients in both terrestrial and wetland soils (Garnett et al. 2017; Xu et al. 2018; Viglizzo et al. 2019; Tessema et al. 2020; Limpert et al. 2021), biodiversity maintenance in rangelands and wetlands (Johnson 2019; Kovácsné Koncz et al. 2020; de Paz et al. 2020; Barry and Huntsinger 2021), as well as facilitate the restoration of otherwise degraded agricultural rangelands (Teague and Barnes 2017; Teague and Kreuter 2020). For ruminant livestock to occupy a sustainable agroecological system that sponsors its own functioning and uses resources efficiently, it is fundamental that there is sufficient knowledge of local ecosystem dynamics (Aswani et al. 2018; Marandure et al. 2018; Pigford et al. 2018)

In South Africa, livestock farming is seminal to small holder farmers in rural areas (Dovie et al. 2006) and contributes to the livelihoods of more than 52.5 million livestock keepers (Gwiriri et al. 2019). Over 90% of livestock keepers in South Africa are classified as smallholder farmers, owning roughly 75% of the livestock in the region (Nyamushamba et al. 2017), of which the Eastern Cape accounts for the highest population (24%) of the total South African cattle population.

In South Africa, there are large areas (69% of the 82% total arable land surface) suitable for livestock (DAFF 2018). It is recognised that there is vast untapped potential for livestock to contribute to economic and food security of rural livelihood in this region (Vetter 2013, Gwiriri et al. 2019). In this regard, livestock-based livelihoods can drive inclusive, climate resilient economic development in the Eastern Cape (Gwiriri et al. 2019). However, it is fundamental that in this region, assessing such targets of sustainability are approached from a system-specific perspective (Marandure et al. 2018).

Chintsa Bay, Eastern Cape, South Africa, occupies the coastal plains of the Eastern Coastal Belt Ecoregion (ECBE), and marks the southern limit of the Savanna Biome (largest Biome in Africa). The transitional nature of this area lends itself to many vegetation types, driven by amount and type of disturbance (Mucina and Rutherford 2006). For example, deep valleys generally exclude fire, encouraging large forest patches with a dense thicket buffer. However, on the adjacent plateau, frequent grazing and fire maintain productive Savanna-type rangelands where the exclusion of such disturbance results in a thicket dominated area. In these agricultural rangelands, natural grazing and fire regimes are modified and controlled by agricultural management. In this way, the area is well suited for extensive ruminant livestock production where appropriate management is the key to its environmental sustainability. Small perennial waterbodies are a common feature in these agricultural grazing areas, providing valuable ecosystem and agricultural services. Gathering regionally specific information on the best-practise indicators and management is a valuable step toward incorporating and restoring agroecological systems in the area.

Identifying regionally significant hydrogeomorphological features supports aquatic biodiversity conservation and waterscape resilience

Perennially inundated waterbodies within grazing areas of the Eastern Coastal Belt Ecoregion (ECBE), collectively termed rangeland waterscapes, occur in a variety of hydrogeomorphic formats. When occurring naturally, they are predominantly deposition pools in river and tributary channels. These pools are abundant, connected by short, intermittently flowing sections. The pools are used by grazing livestock and local indigenous lotic biota. They offer vital habitat and drinking water during the drier winters. Artificial water storage and control features within stream channels, like weirs and dams, are usually constructed by modifying the stream channel to build up a head of water. They replace naturally occurring deposition pools, often completely modifying local and surrounding environmental components (Brasil et al. 2021). Naturally occurring depressions in this area are less common, and are mostly seasonal, unless there are consistent years of high rainfall. However, artificial depressions constructed by excavating shallow contoured features outside of stream channels are common and valuable agricultural structures that are a novel source of perennial lentic habitat in the region.

The results from this study highlight the conservation value of minimally disturbed, small, and well forested deposition pools within tributary channels for range limited, sensitive, and threatened lotic biota in the region. Similar results are replicated across the globe, suggesting that these aquatic habitats, with compositionally and structurally diverse indigenous woody riparian climax vegetation components, like undisturbed primary forest, are inimitable. However, they are being lost at an unprecedented rate, leading to the conclusion that this global landscape pattern needs urgent attention (Dolný et al. 2021). By conserving the integrity of these pools, there is maintenance of perennial sources of clean drinking water for grazing livestock, making them irreplaceable features within a rangeland waterscape.

Yet I found here that well-managed artificial depressions and stream channel water level management features can be complementary sources of perennial water in a rangeland waterscape. These modifications add to both aquatic biodiversity conservation and provide clean drinking water to grazing livestock. At an individual waterbody level, these results are like other studies globally and in South Africa, which illustrate the potential complementarity of artificial depressions as suitable lentic habitats (French and McCauley 2018; Deacon et al. 2018; Harabiš and Dolný 2018; Samways et al. 2020).

Considering and incorporating this regional information at a waterscape management level can maximise the availability of good quality perennial surface water, as well as reduce sensitivity to disturbance. For example, during good rainfall years, ruminant livestock can frequent artificial depressions within the waterscape, avoiding unnecessary disturbance to deposition pool habitats. These waterbodies can be carefully managed, and water levels maintained by stream channel weir systems. During prolonged dry periods, when artificial depressions are dry and weir level low, animals can drink directly from small deposition pools in the tributary channels. This kind of resilience to drought is important in South Africa and is a valuable step toward successful integration of social and economically beneficial agriculture into local ecological systems.

Local biological characteristics assist waterscape management

Biological indicators are used to assess the state of ecosystem health. In freshwater ecosystems, invertebrates are often used as indicators because they are sensitive to environmental changes and are well-studied taxonomically (Jackson et al. 2016). Predators are also good indicators of ecosystem state as they play an important part in maintaining ecological integrity of food webs, structuring prey communities and population dynamics, and are often the first to disappear with major disturbances (Modiba et al. 2017). In South Africa, the South African Scoring system (SASS; see Dickens and Graham (2002)), uses invertebrates, analysed by specialists, to determine the relative aquatic health of lotic ecosystems. This method is a valuable tool but is exclusive and inappropriate for intermittent streams or lentic habitats (Watson and Dallas 2013).

Dragonflies (Odonata), including both damselflies (Zygoptera) and dragonflies (Anisoptera) (both groups of which are here called 'dragonflies'), are excellent indicators of lentic and lotic habitat quality. As a group, they are used globally in assessments, as they are highly sensitive to local environmental changes, well studied taxonomically, highly visible, widely distributed, and have life cycles with both aquatic (larval) and terrestrial (adult) stages (Vorster et al. 2020). Adults are highly mobile, and respond to changes in a landscape, whether improving or deteriorating, shaping resident assemblage composition (Kietzka et al. 2017; Kietzka et al. 2018; Deacon et al. 2020; Sugiman et al. 2020; Worthen and Chamlee 2020; Bastos et al. 2021; Dolný et al. 2021). The Dragonfly Biotic Index (DBI), (see Samways and Simaika (2016)), uses the range of sensitivities within the dragonfly assemblage to assess water quality and biotic value of local water systems. The DBI uses an additive value based on each species' sensitivity to disturbance, geographic range, and International Union for the Conservation of Nature (IUCN) Red List status to assign each species a particular DBI score. The total assemblage composition DBI score (i.e., the total of all the species' scores at one place and time) is then divided by the species richness to give a DBI/site score which can be used to compare sites in the same region (Samways and Simaika 2016). This index can be used by non-specialists, provided there is an understanding of the environmental drivers of regional odonatan assemblage composition. With this kind of regional information, farmers can have a better understanding to formulate strategies for conservation management.

The results from this study show that there are indeed sets of regionally specific dragonfly indicators in the coastal plains of the Eastern Coastal Belt Ecoregion. These regional indicators are valuable in determining baseline ecosystem health, as they illustrate specific components of environmental impact, as well as measure successful restoration efforts. For instance, in river deposition pools, *Crocothemis sanguinolenta* was indicative of relatively good water quality in all hydrogeomorphic waterbody types, while *Chlorolestes tessellatus* is a reliable indicator of good quality riparian habitat in deposition pools in region. Similarly, in depressions, there was different non-overlapping compositional species assemblages, with sensitive and range restricted dragonflies' representative of well-managed waterbodies. In contrast, highly disturbed waterbodies with low ecological integrity were characterised by a species suite of geographically widespread habitat generalists.

This study provides the first set of comprehensive, citizen- and farmer-user guidelines for the application of biological indicators of waterbody quality in the coastal plains of the ECBE. These system-specific indicators not only assist conservationists in determining baseline ecological function to assist in waterscape restoration, but also enable farmers to have tangible indicators that they can use independently.

Conservation recommendations for management and conservation of rangeland waterscapes globally and in the Eastern Coastal Belt Ecoregion.

In general, this study highlights the significance of management strategies that mimic and restore characteristics of naturally occurring, healthy waterscape ecosystems, limit channel modification, and incorporate grazing regimes that reduce the intensity and frequency of disturbances. This holistic management approach to waterscape health is supported by studies globally, having profound implications for restoring ecosystem services like biodiversity conservation, regulation of water supply, erosion control, carbon sequestration, provisioning of livestock products, provisioning of wood products, provisioning of non-wood products, as well as nature-based tourism, building agroecological resilience, and ultimately improving economic gains in otherwise degraded agricultural landscapes (Chien et al. 2019; Turpie et al. 2021). For example, studies show that excluding livestock disturbance or suitable management of grazing intensity results in improved water quality, greater structural and compositional diversity of riparian vegetation, and supports greater assemblage composition diversity of aquatic biodiversity (Cole et al. 2020; Horak et al. 2020; Limpert et al. 2021). This is also the case for constructed wetlands used to filter nutrients from agricultural runoff (Huikkonen et al. 2020). In this regard, there is potential for livestock to be used restoratively and the urgency of addressing ecosystem restoration has been highlighted by the United Nations Decade on Ecosystem Restoration 2021-2030 (United Nations 2021).

For effective rangeland waterscape conservation in the Eastern Coastal Belt Ecoregion, the full range of hydrogeomorphic features needs to be assured, managed, and conserved. This waterbody hydrogeomorphic heterogeneity is fundamental for biodiversity conservation and waterscape resilience. To ensure that all hydrogeomorphic features are conserved, channel modification must be avoided within smaller tributary stream channels. Livestock should be allowed to frequent these deposition pools as an alternative source of drinking water when necessary (i.e. dry season in drought years). In tributary channels, restoration efforts need to focus on clearing of alien vegetation, facilitation of indigenous forest growth, reduction in artificial pool size and maintenance of natural flow regime. The presence of *Chlorolestes tessellatus* yet reduction of sun tolerant, lentic dragonflies like *Ischnura senegalensis, Sympetrum fonscolombii, Lestes tridens, Ceriagrion glabrum, Crocothemis erythreaea, Anax imperator* and *Trithemis arteriosa,* can be used to indicate successful restoration in the region.

In and along major rivers, channel modification should also be avoided where possible to ensure that river deposition pool habitats are not transformed into lentic-like systems. Avoiding this type of habitat transformation is imperative for the conservation of lotic biodiversity. The intensity and frequency of disturbance from grazing livestock should also be limited to improve water quality, diversity of marginal and riparian vegetation structure and composition, and to maintain flow dynamics for appropriate sediment deposition. *Pantala flavescens* can be used to indicate lotic transformation and the overall decline of deposition pool habitat quality in the region. Restoration efforts should focus on water quality remediation, alien vegetation clearing, and riparian forest/thicket mosaic, and buffer system facilitation, from both an individual pool and riverscape perspective.

With appropriate and carefully considered management, water level control features, like weirs, can provide a source of drinking water for livestock troughs, refugia for sensitive biota, and can play a significant role in the restoration of severely eroded river channels. It is imperative here that weirs resemble natural deposition pools by maintaining a natural flow regime and permitting movements of anadromous biota (e.g., Anguillidae spp.). This is fundamental for maintenance of hydrological regime and riverscape connectivity.

Artificial depression waterbodies outside of stream channels can be encouraged as a primary source of drinking water for ruminant livestock. These waterbodies should be widespread across the landscape to offer multiple drinking spots for grazing animals. The relatively short distance between, and the abundance of depression waterbodies in a waterscape is a significant contributor to lentic biota population health, especially in assisting the dispersal of damselflies (Le Gall et al. 2017; Lamelas-López et al. 2021). The quality of water and habitat available to individual waterbodies can be maximised by incorporating a solid woody riparian component. Heterogeneity of macrophytes will also contribute resilience in the system. These positive effects of macrophyte diversity have been documented globally (Law et al. 2019) and in other areas of South Africa (Janssen et al. 2018; Briggs et al. 2019; Jooste et al. 2020).

In a world where human food requirements drive unprecedented impacts on freshwater ecosystems, it is important that we become more in touch with how healthy ecosystems produce food. This understanding both academically and practically is vital to sustaining human existence on this planet. This thesis demonstrates that incorporating vigorous, low impact agriculture into healthy ecological systems requires extensive knowledge and familiarity of the local agro-ecological environment, where context specific information is inimitable.

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